

UC-NRLF



\$C 36 127

LIBRARY
OF THE
UNIVERSITY OF CALIFORNIA.

BIOLOGY
LIBRARY
G

Class

THE GROUSE IN HEALTH AND IN DISEASE

VOLUME I

Univ. of
California

THE
PUBLISHED
BY THE
PUBLISHED

Frontispiece.

(P.Z.S. 1910. Pl. LXXVIII.)



Andre & Sleigh, Ltd.

PAIR OF RED GROUSE IN SUMMER WITH YOUNG CHICKS.

THE GROUSE IN HEALTH AND IN DISEASE

gt. Brit.
"J"
BEING THE FINAL REPORT OF THE
COMMITTEE OF INQUIRY ON GROUSE DISEASE

VOLUME I

WITH 59 FULL PAGE PLATES, MOSTLY IN COLOUR
AND 31 ILLUSTRATIONS IN THE TEXT

LONDON

SMITH, ELDER & CO., 15 WATERLOO PLACE

1911

[All rights reserved]

Univ of
California

5995
G7
v.1

BIOLOGY
LIBRARY

THE GROUSE IN HEALTH AND IN DISEASE

BEING THE FINAL REPORT OF THE
COMMITTEE OF INQUIRY ON GROUSE DISEASE

VOLUME I

WITH A CHAPTER ON THE
HISTORY OF THE GROUSE

LONDON

SMITH, ELDER & CO. 14 WATERLOO PLACE

1911

(Printed in Great Britain)

DEDICATED BY GRACIOUS PERMISSION

TO

His Majesty the King.

TABLE OF CONTENTS

VOLUME I.

CHAPTER	PAGE
Introduction.—By LORD LOVAT	xi
PART I.— <i>THE NORMAL GROUSE.</i>	
I.—The Systematic Position of the Grouse. By A. H. EVANS	1
II.—The Life History of the Grouse. By A. S. LESLIE	5
III.—The Changes of Plumage in the Red Grouse in Health and in Disease. By EDWARD A. WILSON	29
PART I.—PLUMAGE CHANGES IN THE COCK.	
PART II.—PLUMAGE CHANGES IN THE HEN.	
PART III.—LOCAL VARIATIONS IN THE PLUMAGE OF THE GROUSE.	
IV.—Food of the Red Grouse	67
PART I.—OBSERVATIONS ON THE FOOD OF GROUSE, based on an examination of crop contents. By EDWARD A. WILSON.	
PART II.—THE INSECT FOOD OF GROUSE CHICKS, based on an examination of crops and gizzards. By PERCY H. GRIMSHAW.	
PART III.—WATER. By A. S. LESLIE.	
PART IV.—GRIT. By Dr H. HAMMOND SMITH AND R. H. RASTALL.	
V.—Physiology and Anatomy of the Red Grouse. By EDWARD A. WILSON	100
VI.—The Weight of Grouse. By EDWARD A. WILSON	130
PART II.— <i>THE GROUSE IN DISEASE.</i>	
VII.—Causes of Mortality in the Red Grouse. By LORD LOVAT and EDWARD A. WILSON	147
VIII.—Causes of Mortality in the Red Grouse— <i>continued.</i> By EDWARD A. WILSON	152
PART I.—THOSE REFERABLE TO ARTIFICIAL CONDITIONS.	
PART II.—THOSE REFERABLE TO NATURAL CAUSES.	
IX.—Grouse Disease. By EDWARD A. WILSON and A. S. LESLIE	185
HISTORY OF GROUSE DISEASE with an account of the work of the Grouse Disease Inquiry in respect of previous work done by Professor Klein, Dr Cobbold, and others.	

CHAPTER	PAGE
X.—Grouse Disease— <i>continued</i> —Strongylosis	207
PART I.—THE THREADWORMS (<i>NEMATODA</i>). By Dr A. E. SHIPLEY.	
PART II.—ON THE DEVELOPMENT AND BIONOMICS OF <i>TRICHOSTRONGYLUS PERGRACILIS</i> . By Dr R. T. LEIPER.	
XI.—Grouse Disease— <i>continued</i> —Coccidiosis. By Dr H. B. FANTHAM	235
PART I.—THE MORPHOLOGY AND LIFE HISTORY OF <i>EIMERIA</i> (<i>COCCIDIUM</i>) <i>AVIUM</i> , a sporozoön causing a fatal disease among young Grouse.	
PART II.—EXPERIMENTAL STUDIES ON AVIAN COCCIDIOSIS, especially in relation to young Grouse, fowls, and pigeons.	
PART III.—COCCIDIOSIS IN GAME BIRDS AND POULTRY: Some Preventive Measures and Treatment.	
XII.—Grouse Disease — <i>continued</i> —Pathology. By Dr L. COBBETT and Dr G. S. GRAHAM-SMITH	273
XIII.—Observations on the Blood of Grouse. By Dr H. B. FANTHAM	308
XIV.—Observations on the Parasitic Protozoa of the Red Grouse (<i>Lagopus</i> <i>scoticus</i>) with a Note on the Grouse Fly. By Dr H. B. FANTHAM	318
XV.—The Tapeworms (<i>Cestoda</i>) of the Red Grouse (<i>Lagopus scoticus</i>). By Dr A. E. SHIPLEY	334
XVI.—The Ectoparasites of the Red Grouse (<i>Lagopus scoticus</i>). By Dr A. E. SHIPLEY	347
PART III.—MANAGEMENT AND ECONOMICS OF GROUSE MOORS.	
XVII.—Moor Management. By LORD LOVAT	372
XVIII.—Heather-burning. By LORD LOVAT.	392
XIX.—The Heather Beetle. By P. H. GRIMSHAW	414
PART I.—ON "FROSTED" HEATHER AND ITS CONNECTION WITH THE HEATHER BEETLE (<i>LOCHMÆA SUTURALIS</i>).	
PART II.—THE LIFE HISTORY OF THE HEATHER BEETLE.	
XX.—Keepers and Keeping, with sub-divisions dealing with Poachers and Vermin. By LORD LOVAT	430
XXI.—Stock. By LORD LOVAT	454
XXII.—Grouse in Captivity. By Dr H. HAMMOND SMITH	483
XXIII.—Value of Grouse Shootings in Great Britain By A. S. LESLIE	491
Index	503

LIST OF ILLUSTRATIONS

PLATE

I. PAIR OF RED GROUSE IN SUMMER WITH YOUNG CHICKS	<i>Frontispiece</i>
II. MALE GROUSE, BLACK TYPE, IN FULL WINTER PLUMAGE	<i>to face page</i> 34
III. MALE GROUSE, RED TYPE, IN FULL WINTER PLUMAGE	" 34
IV. MALE GROUSE, WHITE SPOTTED BIRD OF RED TYPE	" 34
V. MALE GROUSE, RED TYPE, IN FULL WINTER PLUMAGE WITH A FEW BLACK CENTRED FEATHERS OF THE PREVIOUS AUTUMN PLUMAGE	" 35
VI. MALE GROUSE SHOWING MARKED BEGINNING OF THE AUTUMN PLUMAGE ON HEAD AND NECK	" 36
VII. MALE GROUSE CHANGING FROM WINTER TO AUTUMN PLUMAGE	" 36
VIII. FEMALE GROUSE, BLACK TYPE, IN AUTUMN PLUMAGE	" 44
IX. FEMALE GROUSE, RED TYPE, CHANGING FROM WINTER TO SUMMER PLUMAGE	" 45
X. FEMALE GROUSE IN FULL BREEDING PLUMAGE	" 45
XI. FEMALE GROUSE IN FULL SUMMER PLUMAGE	" 46
XII. FEMALE GROUSE, RED TYPE, FEATHERS FROM FLANKS	" 46
XIII. FEET OF RED GROUSE: (1) NEW WINTER FEATHERS AND NAILS; (2) FULL WINTER PLUMAGE; (3), (4), (5) AND (6) SHOWING STAGES IN MOULTING OF NAILS	" 46
XIV. FEMALE GROUSE, SHOWING BARE PATCH OF SKIN AND DOUBLE LINE OF BARRED FEATHERS ON ABDOMEN	" 47
XV. FEMALE GROUSE, RED TYPE, WORN UPPER TAIL COVERTS	" 47
XVI. HEADS OF (1), (2), FEMALE GROUSE; (3), (4), MALE GROUSE; (5) PTARMIGAN SHOWING SUPRA-ORBITAL COMBS	" 48
XVII. HEAD OF BLACKCOCK SHOWING SUPRA-ORBITAL COMB	" 49
XVIII. MALE GROUSE SHOWING ABNORMAL ERYTHRISM	" 60
XIX. FEMALE GROUSE, BUFF-BARRED TYPE	" 60
XX. FEMALE GROUSE, ABNORMAL YELLOW VARIETY	" 60
XXI. FEMALE GROUSE, GREY VARIETY	" 60
XXII. FEMALE GROUSE, GREY VARIETY	" 60
XXIII. TYPES OF HEATHER	" 71
XXIV. PLANTS EATEN BY THE GROUSE (4 Figures)	" 86
XXV. PLANTS EATEN BY THE GROUSE (4 Figures)	" 87
XXVI. DIAGRAM OF ALIMENTARY TRACT	" 101
XXVII. ALIMENTARY TRACT, CÆCUM, RECTUM, GIZZARD, DUODENUM, SMALL INTESTINE	" 102
XXVIIa. ALIMENTARY TRACT <i>IN SITU</i>	" 103
XXVIII. CÆCUM, DUODENUM, ETC.	" 104
XXIX. RECTUM AND SMALL INTESTINE	" 115
XXX. CÆCA	" 117
XXXI. CÆCA AND KIDNEYS	" 118
TEXT-FIG. 1. FRACTURED HUMERUS AND SCAPULA RE-UNITED	<i>page</i> 154
" 2. THE SAME BONES UNINJURED	" 154
" 3. FRACTURED AND RE-UNITED BREASTBONE OF A GREY HEN	" 158

PLATE		
TEXT-FIG. 4, 5. FRACTURED AND RE-UNITED BREASTBONE—VIEWS OF RIGHT AND LEFT SIDE		Page 159
„ 6. FRACTURED AND RE-UNITED BREASTBONE SHOWING METHOD OF UNION	„	160
„ 7, 8. BROKEN AND RE-UNITED WING-BONES	„	162
„ 9-11. BROKEN AND RE-UNITED LEG-BONES	„	163
„ 12-15. BROKEN AND RE-UNITED THIGH-BONES	„	164
XXXII. BUMBLEFOOT IN GROUSE	to face page	170
XXXIII. <i>TRICHOSTRONGYLUS PERGRACILIS</i> AND <i>TRICHOSOMA LONGICOLLE</i> (5 Figures)	„	209
TEXT-FIG. 16. MORULÆ IN EGG OF <i>TRICHOSTRONGYLUS PERGRACILIS</i>	page	219
„ 17, 18. DEVELOPING OVA OF <i>T. PERGRACILIS</i>	„	221
„ 19, 20, 21. FORMATION OF THE LARVA OF <i>T. PERGRACILIS</i>	„	221
„ 22, 23. EMBRYOS OF <i>T. PERGRACILIS</i> HIGHLY MAGNIFIED	„	223
„ 24-27. CHANGES IN <i>T. PERGRACILIS</i> DURING ECDYCSIS AND ENCYSTMENT	„	225
„ 28, 29. LARVAL FORMS OF <i>T. PERGRACILIS</i>	„	227
„ 30. ENCYSTED LARVÆ OF <i>T. PERGRACILIS</i>	„	227
XXXIV. <i>EIMERIA</i> (<i>COCCIDIUM</i>) <i>AVIUM</i> (SCHIZOGONY)	to face page	238
XXXV. <i>EIMERIA</i> (<i>COCCIDIUM</i>) <i>AVIUM</i> (MACROGAMETE FORMATION)	„	240
XXXVI. <i>EIMERIA</i> (<i>COCCIDIUM</i>) <i>AVIUM</i> (MICROGAMETES SPOROGONY)	„	243
XXXVII. <i>EIMERIA</i> (<i>COCCIDIUM</i>) <i>AVIUM</i> (SPOROGONY)	„	245
TEXT-FIG. 1. DIAGRAM OF LIFE-CYCLE OF <i>EIMERIA</i> (<i>COCCIDIUM</i>) <i>AVIUM</i>	page	248
XXXVIII. AVIAN COCCIDIOSIS	to face page	252
XXXIX. (1) APPARATUS FOR MAKING CULTURES AND (2) ALIMENTARY CANAL OF GROUSE	„	278
XL. TEST TUBES CONTAINING <i>T. PERGRACILIS</i> (2 Figures)	„	283
XLI. SECTIONS OF CÆCUM SHOWING <i>T. PERGRACILIS</i> (6 Figures)	„	285
XLII. <i>T. PERGRACILIS</i> AND <i>D. UROGALLI</i> (4 Figures)	„	287
XLIII. SECTIONS OF CÆCUM (6 Figures)	„	288
XLIV. DIAGRAM OF ALIMENTARY CANAL SHOWING HABITATS OF INTESTINAL PARASITES	„	290
XLV. BLOOD CELLS OF BIRDS CHIEFLY OF GROUSE	„	309
XLVI. <i>LEUCOCYTOZOÏN LOVATI</i>	„	319
XLVII. <i>LEUCOCYTOZOÏN LOVATI</i> , <i>SPIROCHÆTA LAGOPODIS</i> AND <i>HÆMOPROTEUS MANSONI</i>	„	320
XLVIII. <i>TRICHOMONAS EBERTHI</i> , <i>SPIROCHÆTA LOVATI</i> , <i>AMŒBA LAGOPODIS</i>	„	326
XLIX. <i>DAVAINEA UROGALLI</i>	„	335
L. <i>D. UROGALLI</i> AND <i>HYMENOLEPIS MICROPS</i>	„	336
LI. <i>D. UROGALLI</i> , <i>HYMENOLEPIS MICROPS</i> , ETC. (7 Figures)	„	337
LII. <i>HYMENOLEPIS MICROPS</i>	„	342
LIII. <i>GONIODES TETRAONIS</i> (4 Figures)	„	350
LIV. <i>NIRMUS CAMERATUS</i> (2 Figures)	„	357
LV. <i>ORNITHOMYIA LAGOPODIS</i> (3 Figures)	„	358
LVI. <i>CERATOPHYLLUS GALLINULÆ</i> , ETC. (3 Figures)	„	361
LVII. HEATHER GROWING FROM THE ROOT AND FROM SEED	„	401
LVIII. THE HEATHER BEETLE (<i>LOCHMÆA SUTURALIS</i>) (4 Figures)	„	426

INTRODUCTION

By Lord Lovat

BEFORE the formal appointment of the Committee in 1905 the following preliminary work of organisation was carried out.

On June 5th, 1904, the organisers of the present investigation met, and after discussion formed a Committee of Inquiry to investigate the subject of "Grouse Disease." The following gentlemen were present: The Marquis of Tullibardine, Lord Lovat, Mackintosh of Mackintosh, Mr R. H. Rimington Wilson, Mr J. Graham, Mr D. W. Drummond, Mr R. C. Munro Ferguson.

Lord Lovat was appointed Chairman, and Lord Onslow, the then President of the Board of Agriculture, was approached with the view of obtaining the assistance of that Board.

A further meeting was held in December of the same year, when the details of the proposed lines of inquiry were discussed, a Secretary was appointed, and a number of witnesses were examined. The formal appointment of the Committee as a Departmental Committee of the Board of Agriculture and Fisheries was intimated by the Secretary of the Department on April 13th, 1905. The terms of the appointment marked a departure from the usual procedure in such matters, for they provided that no public funds should be devoted to the Inquiry, but that the investigation should be conducted at the expense either of the members of the Committee or of private subscribers. The members included the above-named gentlemen, with the addition of Earl de Grey (now Marquis of Ripon) and Lord Henry Scott. Dr William Somerville was appointed to represent the Board of Agriculture and Fisheries, and upon his retirement from the Board Mr T. H. Middleton was appointed. The Committee sustained a severe loss by the death in 1910 of Mr James Graham, one of its most active and capable members.

In April and May 1905 an appeal was sent to a limited number of proprietors and tenants of Grouse moors asking for financial support. This appeal resulted in subscriptions amounting to over £400; these subscriptions were limited to a sum

not exceeding £5 a year, and in the majority of cases were guaranteed for a period of three years. On the strength of this response a number of scientific gentlemen were asked to assist in the investigation, and a body of local correspondents in different parts of the country was appointed to make observations and to report upon any special local conditions or circumstances affecting Grouse in their respective districts. These local correspondents consisted mainly of resident proprietors, factors, estate agents, and gamekeepers. Great care was taken in their selection, and experience has shown that they have fully justified their appointment. About three hundred correspondents were formally appointed, and many other proprietors and gamekeepers corresponded regularly with the Secretary and with the staff of the Committee whenever occasion arose. The list of local correspondents might easily have been doubled by adding to it the names of those who had shown themselves able and willing to assist the investigation, but unfortunately the funds of the Committee would not admit of such addition. Lists of the Committee, of the staff, and of the local correspondents are given in Appendix A.

For the instruction of local correspondents and others who wished to be informed of the existing state of knowledge on the subject of "Grouse Disease," and further to indicate the exact points upon which information was required, the Committee drew up an illustrated pamphlet entitled "Notes on the Grouse"; in this a short summary was given of the life history of the bird, with a description of the typical characteristics of "Grouse Disease" as then recognised. The pamphlet called attention to the many theories which existed on the subject, and indicated the lines upon which the Committee proposed to carry out their investigation. This pamphlet was privately circulated among correspondents and subscribers, but was not offered for sale.

The scientific experts drew attention to the difficulty of carrying out experiments upon Grouse in a wild state, and accordingly in 1906 the Committee established an observation area in Surrey, where it was soon demonstrated that Grouse could be kept in captivity. The necessary licence was obtained from the Home Office. This observation area has been of the utmost value to the Committee.

Owing to the necessity of having a constant supply of healthy Grouse for examination in every month of the year, to enable the Committee to collect accurate information on the question of feeding, moulting, and seasonal changes, arrangements were made by members of the Committee and certain local correspondents to send to the Field Observer each month of the year a certain number of freshly killed birds. Many hundreds of such birds have been examined, and

from the material so obtained valuable, and in many cases new information was gained. An interesting collection of over six hundred Grouse skins has been prepared, showing the types of plumage found in both sexes at different times of the year and in different districts, and also certain abnormalities. Selections from this collection and from the other material collected by the Committee were exhibited at a soirée of the Royal Society in May 1909, and at the Vienna Sports Exhibition of 1910.

The Committee began their observations in the field in the autumn of 1905; during this season and 1906 the stock of Grouse both in Scotland and England was remarkably healthy, and an excellent opportunity was thus given to study the bird under normal conditions. The Field Observer visited many moors, his visits extending over a period of seven months, from April to October. During this time he got into close touch with the Committee's correspondents in different parts of the country, checked their information, and with their assistance studied the varying conditions governing particular districts. Whenever a case of suspected "Grouse Disease" was reported the moor was visited by the Field Observer or one of his assistants, and specimens of suspicious birds were subjected to laboratory examination.

During 1907 a considerable mortality amongst the Grouse in certain districts was reported in the spring and early summer months. The Committee's experts made a very careful investigation into every case reported, but, contrary to expectation, it was not found that the character of the disease differed materially in its essential features from those occasional isolated cases of mortality which had occurred in the previous year. The Committee found no examples of the acute or sudden form of disease which had been described by former observers. The outbreak of mortality, however, gave an excellent opportunity for collecting data regarding the lingering or pining form of disease which has since been traced to the ravages of the threadworm *Trichostrongylus pergracilis*.¹

By 1908 the Committee had completed the preliminary work required to enable the subject to be developed on scientific lines. Evidence and statistics had been collected which indicated the special directions in which further investigations were necessary or likely to be helpful. The natural history of the normal healthy Grouse had been fully studied, and the general pathological characteristics of "Grouse

¹ In the following chapters this worm is usually called *Trichostrongylus pergracilis*, but some writers have preserved *Strongylus pergracilis*, it is also at times called the Strongyle or the Strongyle worm. A synonym and a list of allied species are given by Dr Shipley on pp. 207 *et seq.*

Disease," from a field observer's point of view, had been ascertained. Even at this date the Committee were of opinion that they had discovered the principal causes of mortality amongst Grouse; but until they had further confirmed their suspicions they decided not to publish anything in the nature of results. It was at this stage that an impatient public and the necessity to stimulate dilatory subscribers forced upon the Committee the necessity of publishing some account of their progress, and the Interim Report issued in August 1908 was the outcome of this demand. The Interim Report contained an account of the work done by the Committee up to date, but omitted all reference to the results which had only been achieved in part.

During the second or research stage of the investigation the following special points were studied: (1) The life history of the *Trichostrongylus pergracilis*, which the Committee believed to be the immediate cause of "Grouse Disease"; (2) The life history of the other internal parasites of Grouse; (3) The protozoal parasites infecting the alimentary tract and blood of Grouse; (4) The bacteriology of Grouse; (5) The various insects found on the moors both from the point of view of insect-borne disease and from the point of view of food; (6) The questions affecting the food supply of Grouse, including the management of heather land, causes of destruction of heather, *e.g.*, frost, heather-beetle, etc.

These lines of research were diligently followed up by the members of the Committee's Scientific Staff during the last three years of the Inquiry—the work entailed long series of experiments carried out upon the open moor, in the laboratory, or at the Frimley observation area. The results have been unexpectedly conclusive, considering the short time available for so great a task.

The Committee consider that although their immediate object has been achieved, *viz.*, the elucidation of the causes of "Grouse Disease," the present Inquiry has scarcely crossed the threshold of the investigation into the general pathology of birds, and there is still a large amount of work which might be profitably undertaken. The most important department of the research, so far at least as relates to mortality amongst adult Grouse, was the investigation of the life history of the strongyle threadworm. The work was rendered difficult owing to the small size of this parasite, but thanks to the efforts of Dr Wilson, Dr Shipley, and Dr Leiper, we are now in a position to speak with something approaching certainty on the subject. These gentlemen have worked at the subject for more than three years, and have not only ascertained the life cycle through which this worm passes, but have discovered the conditions which are favourable or preju-

dicial to its growth; they have been able to rear the young strongyle, and by administering it through the medium of food to hand-reared Grouse free from nematode infection, have infected the hand-reared birds with "Grouse Disease."

Another interesting and important outcome of the Inquiry has been the discovery of a cause of death among Grouse in their infancy due to the presence of an intestinal parasite known as *Eimeria (Coccidium) avium*. It is unfortunate that the Inquiry is being brought to a close while Dr Fantham is still engaged in tracing the predisposing causes of this disease with a view to finding whether any preventive measures are possible. It is true that such preventive measures, even when found, might not be easily applied to the Grouse in a wild state; but they would be of the greatest possible value for the treatment of hand-reared game-birds or domestic fowls.

During the progress of the Inquiry many questions affecting Grouse and Grouse shooting, but not directly connected with disease, have come before the notice of the Committee, and owing to their general interest to readers of the Report it has been thought well to refer to some of them. Since the Inquiry has been mainly supported by those whose interests are more intimately connected with sport than with science, the inclusion of chapters on such subjects of practical importance as Moor Management, Heather-burning, Vermin, Keepers and the Value of Grouse moors, requires no apology. The chapters of natural history, such as Life History, Plumage changes, Food, Physiology and Death from Causes other than Disease, are all indirectly connected with the main subjects of the Inquiry.

It will be seen that by the inclusion of the above-mentioned chapters the Report of the Committee becomes a monograph on the Red Grouse in health and disease rather than a summary of the proceedings of a Departmental Committee of Inquiry.

During the period of the Inquiry a large number of Pamphlets, Reports, and Letters of Instructions have been printed and issued by the Committee to its local correspondents and other supporters. These documents, in addition to the "Notes on the Grouse" pamphlet already referred to, include Notes of Evidence taken at the meetings of Committee, Lists of Queries, Forms of Particulars of Specimens, Periodical Reports on the Progress of the Inquiry, Lists of Subscribers, Lists of Local Correspondents, Statements of Crop-contents, Circular Letters to Proprietors, etc., etc. In all more than 40,000 printed documents have been circulated, in addition to a large number of typewritten circulars and letters, of which no accurate record has been kept.

The correspondence both of the Secretary and the Field Observer has been

voluminous, and has sometimes been subject to such sudden bursts of activity that it was found well-nigh impossible to keep pace with it. To this cause must be ascribed occasional failures to acknowledge written communications by return of post, for which failures the Committee now tender their apology.

In the course of the investigation many technical questions arose which made it necessary to employ the services of leading scientific experts, and, owing to the difficulty in obtaining immediate and definite results, it was found that the period of the Inquiry would have to be extended beyond the three years originally fixed. The result has been that the Committee found it necessary to exceed their original estimates.

During the whole Inquiry the Committee has been greatly hampered in their labours by lack of funds. The total income has never amounted to £1,000 in any one year, and the work would have been in danger of coming to an end were it not that many members of the Scientific Staff have given their services gratuitously or for at most a nominal consideration.

What success the Committee have met with is due to several causes. Firstly, the work was, in the main, directed by small Sub-Committees who were unhampered by official restrictions and untrammelled by traditional red tape. Secondly, the Chairman and the Secretary had the cordial support not only of the other members of the Committee but of all those directly or indirectly interested in the Grouse. Thirdly, the members of the Scientific Staff took the keenest interest in the problems they sought to solve, and were willing to place their knowledge, their spare time, and their technical skill at the disposal of the Committee unremunerated, or at best remunerated at an entirely inadequate scale. Fourthly, the Inquiry aroused a certain public spirit, which not only found expression in the willingness of sportsmen, landlords, keepers, and others to do all in their power to assist the work of the Committee, but led the printers, the firm which supplied the paper upon which the book is printed, the publishers and many others connected with the preparation of the volume, to grant the Committee the most favourable terms.

That this Inquiry did not cost more than the small sum of £4,366 in the six years over which the work extended (averaging £727 a year) is due to the causes set forth above, and to the constant vigilance and unselfish insistence on economy on the part of the Secretary. Compared with the cost of similar Royal Commissions and Departmental Committees this sum is a mere trifle, but it shows that satisfactory results *can* be attained at very small expense. Much money was of course saved by not printing the evidence given at the numerous examinations of gamekeepers

and others held by the Committee. Such evidence is, as a rule, printed in full, and remains unheeded and unread in tons of neglected Blue-Books. Then again the money has been carefully and laboriously collected, for the Committee were precluded by the terms of their reference from drawing on the purse of the taxpayer. This also made for economy.

Some criticisms have been heard at the delay which has occurred in the production of this volume. But it should be remembered that when the Inquiry started very little was accurately known about the Grouse either in health or in disease. As a member of the Scientific Staff said in a lecture before the Royal Institution: "In considering exceptions it is so immensely important to know the rule. In studying disease our starting-point should be the normal, the healthy; yet until lately no one has closely studied the healthy Grouse, and indeed it is almost impossible to find a normal Grouse, *i.e.*, one free from parasites. A Grouse cannot express to us its feelings; the state of its tongue, the rate of its pulse, even its temperature tell us nothing because we have no norm and no means of estimating the extent to which a diseased Grouse has departed from the standards of a healthy bird. The nature of the numerous kinds of blood corpuscles, which alter in proportion so markedly in animals when they become parasitised, was but a few months ago quite unknown, the "blood count" uninvestigated; in fact the Inquiry started, as regards the cause and symptoms of the diseases which affect Grouse, practically behind scratch."

Further, the Committee were not in a position to retain the whole time of any one of their Scientific Staff with the single exception of the Field Observer. What work this staff have accomplished, and they have accomplished much, has been for the most part done in their spare time or during their brief holidays. Another factor that made for delay was that the Committee were not in a position to establish a central laboratory, and hence the actual investigations were carried on for a time in one place, and then after a break often of many weeks the threads were picked up in another. Much work was done at Cambridge, but at the London School of Tropical Medicine, at the Royal Scottish Museum, Edinburgh, at Frimley, at King's School in the Isle of Man, in the offices of the *Field* in London, in the gun-room at Beaufort, valuable investigations were also carried on. Further, from the necessity of examining absolutely fresh material, an improvised travelling laboratory had to be set up perhaps in a private sitting-room of a country hotel, perhaps in an outhouse of a Highland inn, but always under conditions which vastly increased the difficulty of investigation, and made for delay.

Considering all these circumstances, the results now published do not seem unduly belated.

The Committee specially desire to record their thanks to the following gentlemen who have formed the Scientific Staff of the Inquiry, and to whose labours the results are due :—

EDWARD A. WILSON, M.B., F.Z.S., M.B.O.U., was appointed, in November 1905, principal Field Observer, Anatomist and Physiologist to the Inquiry, and devoted his whole time to the work till the autumn of 1910, when he joined Captain Scott's Antarctic Expedition as Scientific Director on the *Terra Nova*. It is difficult to speak highly enough of Dr. Wilson's services, for not only was he an indefatigable worker in the field, but his ornithological knowledge, his scientific training, and his artistic skill, have been of the utmost value in every branch of the Inquiry. Practically every Grouse which was submitted to the Committee for examination was dissected and reported on by Dr Wilson, and the results of these dissections, as shown in Appendix D, not only form a record of long and patient labour, but also provide an enormous mass of carefully arranged material which has been of great use to the Committee. Dr Wilson has written or aided in writing ten out of the first fourteen chapters of the Book, and has not only fully illustrated his own contributions, but has placed his artistic skill at the disposal of nearly all the other writers. In addition to his services as Field Observer and Physiologist, Dr Wilson conducted a series of experiments on live Grouse at the Committee's Observation Area whereby the results obtained by Dr Leiper, Dr Shipley and others were put to the test; these experiments entailed some years of hard and patient work, and required the closest co-operation with the other members of the Scientific Staff. Dr Wilson's personal qualities secured for him the willing assistance alike of Local Correspondents and Scientific Staff, and went far to ensure whatever success the Committee has achieved.

A. E. SHIPLEY, M.A., Hon. D.Sc., F.R.S., Master of Christ's College, Cambridge, and Reader in Zoology in the University of Cambridge, undertook in June 1905 to assist the Committee in the Scientific Departments of their research, especially in connection with the investigations of the ectoparasites and endoparasites of Grouse. Dr Shipley's services to the scientific side of the Inquiry have been as important as Dr Wilson's services to the natural history side. Dr

Shipley has published the results of his labours in the *Proceedings of the Zoological Society of London* for 1909 in the following series of articles: (1) The Tapeworms (cestoda) of the Red Grouse; (2) The Threadworms (nematoda) of the Red Grouse; (3) The ectoparasites of the Red Grouse; (4) The Internal Parasites of birds allied to the Grouse. The first three of these papers are, by the courtesy of the Zoological Society of London, reprinted with minor alterations in the present Report. Dr Shipley has also acted as one of the Publishing Sub-Committee of the Inquiry, and has given much assistance in the revisal of the proofs and the preparation of Interim and Final Reports for the press.

R. F. LEIPER, D.Sc., M.B., F.Z.S., Helminthologist to the London School of Tropical Medicine, was appointed in 1908 to help in the elucidation of certain difficult questions relating to the life history of the nematode worm *Trichostrongylus pergracilis*, which in the opinion of the Committee is the main cause of mortality in adult Grouse. Dr Leiper devoted much time to the study of these questions, and to him is due the credit of having solved many of the problems connected with the development and bionomics of this important parasite. The result of his investigations are given in the present Report.

W. BYGRAVE and PERCY H. GRIMSHAW assisted Dr Shipley by a prolonged and systematic search for the intermediate host of the Grouse tapeworms, and though the results were negative, the conscientious manner in which the search was conducted has enabled the Committee to claim that the question has been investigated as fully as was possible in the time at their disposal.

H. B. FANTHAM, D.Sc. Lond., B.A. Cantab., A.R.C.S., F.Z.S., Christ's College, Cambridge, Parasitologist to the Liverpool School of Tropical Medicine, formerly Assistant to the Quick Professor of Biology in the University of Cambridge, was appointed Protozoologist to the Inquiry in 1907, and since that date has made a careful study of the protozoal parasites which are found in the blood and alimentary tract of the Grouse. His researches have resulted in a most interesting series of discoveries, of which by far the most important from the Committee's point of view is that the *Eimeria (Coccidium) avium* frequently found in the alimentary tract of the Grouse is a frequent cause of death of young birds. Dr Fantham has followed up and fully described the life history of this parasite, whose presence in the intestine of the young Grouse was first pointed out by Dr. Leiper, and has published the results of his researches in the *Proceedings of the Zoological Society of London* for October 1910 in the following series of articles: (1) The

Morphology and Life History of *Eimeria* (*Coccidium*) *avium*: a Sporozoön causing a fatal disease among young Grouse; (2) Observations on the Parasitic Protozoa of the Red Grouse (*Lagopus scoticus*); (3) Experimental studies on Avian Coccidiosis, especially in relation to young Grouse, Fowls and Pigeons; (4) Observations on the Blood of Grouse. By the courtesy of the Zoological Society of London these articles are reprinted in the present Report.

C. G. SELIGMANN, M.B., then Pathologist to the Zoological Society of London, was appointed in 1906 to investigate the bacteriology of "Grouse Disease." He worked for the Committee till the end of 1907, when he left for Ceylon on a scientific expedition. The Committee is indebted to him for the discovery that the bacterial characters observed by Professor Klein as symptomatic of "Grouse Disease" were not in fact the pathological accompaniment of the mortality in Grouse as observed by the Committee. After Dr Seligmann went abroad his observations on this point were continued and confirmed by Dr Cobbett and Dr Graham Smith.

L. COBBETT, M.D., F.R.C.S., University Lecturer in Pathology, Cambridge, and G. S. GRAHAM-SMITH, M.D., University Lecturer in Hygiene, Cambridge, consented in 1909 to continue the work where Dr Seligmann had left off. They made an exhaustive investigation of the general pathology of "Grouse Disease" in all its forms, and the relation of the *Bacillus coli* of Professor Klein's "Grouse Disease" to the various pathological lesions which had come under the observation of the Committee. The results of their investigations were published in the *Journal of Hygiene* in June 1910, and, by the courtesy of Professor Nuttall, the Editor of that Journal, are reprinted in the present Report.

L. W. SAMBON, M.D., gave considerable assistance to Dr Seligmann during the spring of 1907, and discovered a new leucocytozoon in the blood (*L. Lovati*).

H. HAMMOND SMITH, M.B., Pathologist to the *Field* newspaper, has assisted the Committee both in the field and in the laboratory since the Inquiry was commenced. He established and organised the Observation Area at Frimley in Surrey, and gave great assistance to the Committee in connection with the conduct of experiments at this Observation Area. He also assisted in the study of the question of the grits found in the gizzards of the Grouse and other game birds, and gave great help to the Committee in connection with the conduct of experiments at the Observation Area.

R. H. RASTALL, M.A., F.G.S., Fellow and Lecturer of Christ's College, Cambridge, drew up an interesting report on the mineral constituents of gizzard grits in Grouse, and gave assistance in writing the article dealing with grits which appears in this Report. He also aided the work of publication by reading and correcting almost the whole of the proofs of this Report.

PERCY H. GRIMSHAW, F.R.S.E., F.E.S., Assistant Keeper of the Natural History Department, Royal Scottish Museum, was appointed in 1909 to undertake the whole investigation of the insect life on the moors. He carried on and elaborated the work begun by Mr Fryer and Mr Hill, and not only prepared a complete list of the insects found on the moors, but also reported upon those eaten by the Grouse as shown by an examination of their crops and gizzards. The result of his work is published in the "Annals of Scottish Natural History" for July 1910, and in chapter iv. and Appendix E of the present Report. Mr Grimshaw also undertook the investigation of the habits and life history of the heather beetle (*Lochmaea suturalis*), and his article on this subject is included in the Report.

GEORGE C. MUIRHEAD, B.Sc., acted as Field Observer from May to December 1905, and assisted in drawing up the pamphlet "Notes on the Grouse."

J. C. FRYER, B.A., Gonville and Caius College, Cambridge, was appointed in 1907 to make a report on the Insect Life of Grouse Moors. This Report has already appeared in the Interim Report of the Committee.

ALFRED HILL was employed in 1908 to carry on the investigations already commenced by Mr Fryer.

A. S. LESLIE, B.A., W.S. As soon as the Committee was officially appointed in 1905, one of their first acts was to nominate Mr Leslie as Secretary. During the six years that the Committee have sat he has continued to act in that capacity, and his duties have been both varied and arduous.

To him was entrusted the task of collecting the subscriptions, which formed the sole source of income for the Inquiry, and without which nothing could be done ; the control of this Fund further rested in him. He also got together and organised the three hundred and sixty local correspondents, he drew up all the various tables, forms, etc., with which these correspondents were supplied, received the answers to the questions asked, collated and tabulated not only these answers but the verbal

replies given at the several examinations of gamekeepers and other experts, which from time to time the Committee held. His correspondence amounted to many thousands of letters. Further, he assisted the Field Observer in many ways, especially in the preparation of statistics and the arrangement of tabular matter.

Mr Leslie wrote the "Notes on the Grouse," and has been in the main responsible for the preparation and seeing through the press both the Interim and the present (Final) Report; the compiling of the appendices and the index, and the revision of the proofs, were largely his work.

To his knowledge of Scotland and of sport, and his professional training, the Committee owe many valuable suggestions as to the course the investigations have from time to time taken. They feel they cannot speak too highly of the self-sacrificing way he has thrown himself into the work, of his untiring energy, of his powers of organisation or of his adaptability and tact, which has done much to make the labours of not only the Committee but of all in any way associated with the Inquiry not only profitable but pleasurable.

The salary that the Committee have been able to offer to Mr Leslie can only be described as derisory. He has, in fact, received but the scantiest payment for the work he has done, and no compensation of any kind for the time he has taken from his profession and given to the Inquiry. But not only has he, like others, given time, skill and knowledge to further the cause of the investigation, but by his skilful husbandry of the limited resources available he has enabled the Committee to cover a wider area of research, and to prolong the time during which research was carried on to an extent which at first seemed impossible.

R. B. FRASER was appointed Assistant Secretary in October 1907, when it was found that the work of organisation and correspondence could not be conducted single handed by the Secretary. Mr Fraser has given valuable assistance with the general secretarial work, and also with the additional work entailed in connection with the preparation of the Report for the press.

In addition to those already mentioned the following have given the Committee much assistance in the revisal of proofs and in other ways: W. BERRY, B.A., LL.B., M.B.O.U., who has been chiefly responsible for the Index; W. R. OGILVIE GRANT, M.B.O.U., of the British Museum of Natural History; W. EAGLE CLARK, F.L.S., F.R.S.E., etc., Keeper of the Natural History Department of the Royal Scottish Museum; L. R. SUTHERLAND, M.B., Professor of Pathology in the

University of St Andrews; Mrs E. A. WILSON, and the Hon. GLADYS GRAHAM MURRAY, F.Z.S.

An Abstract of Accounts is annexed, from which it may be seen how the income has been expended.¹

The whole funds have now been exhausted in the work of investigation, and there is no balance available to meet the cost of publishing the results. This is to be regretted, as it will make it impossible to provide the supporters of the Inquiry with copies of the Report free of charge.

The thanks of the Committee are due to those moor-owners, shooting tenants, gamekeepers, and others who have gratuitously given their services as correspondents.

The Committee have to acknowledge with thanks the support it has received from its subscribers. A list of subscribers and the amount of their subscriptions is given in Appendix B.²

The Committee have also to acknowledge their indebtedness to the Zoological Society of London, which at the request of the Committee published in the *Proceedings* of the Society the articles on Ectoparasites and Endoparasites of Grouse by Dr A. E. Shipley; the articles on the Protozoa and Blood of Grouse, by Dr H. B. Fantham; and the article on the Plumage of Grouse, by Dr E. A. Wilson, comprising an important part of the scientific matter contained in this volume, which is reproduced here by consent of the Society. They have also to acknowledge their indebtedness to the Society for revising and editing the manuscript of Dr Wilson's contributions on the Plumage of the Grouse, in the absence of the author on the Antarctic Expedition.

The Committee also desire to acknowledge its indebtedness to the heads of the various Scientific Laboratories at Cambridge, where much of the research work was carried on; to the London School of Tropical Medicine who permitted Dr Leiper to assist in the investigation; and to the Directors and Staff of the Royal Scottish Museum, who assisted the Committee in various ways during the whole period of the Inquiry.

¹ *Vide* vol. ii., Appendix C.

² *Vide* vol. ii., Appendix B.

Library of
Oxford University

THE GROUSE IN HEALTH AND IN DISEASE

PART I.—THE NORMAL GROUSE

CHAPTER I

THE SYSTEMATIC POSITION OF THE GROUSE

By A. H. Evans

THE name Grouse, in the form "Grows," has been traced back by Salusbury Brereton to the reign of Henry VIII. (1531), and in its present form to 1603. But, since it first occurs in an ordinance for the regulation of the Royal Household at Eltham in Kent, it ought in all probability to be applied to the Black Grouse which may then have inhabited that county, though no actual record has yet been discovered. Further particulars are given by Professor Newton in his "Dictionary of Birds."¹ The appellation has, however, by universal consent been long transferred to the Red Grouse, the Moorfowl of our forefathers, and when standing alone would never now be understood otherwise.

History of
the name
Grouse.

This species is the most characteristic bird of the Scottish moorlands, including the Hebrides and the Orkneys, and is plentiful thence to the northern counties of England; in few places is it more numerous than on the moors of South Yorkshire and Derbyshire in the vicinity of Sheffield; while to the west it not only occurs in decreasing numbers to Shropshire, but is found in Wales as far south as Glamorganshire, and in Ireland in most suitable localities. Attempts have been made to acclimatise it to the north and south of its proper range; but the few pairs turned down in Shetland between 1858 and 1883, with a greater number in 1901, have never thriven, while their descendants are apparently extinct, and the same may be said of those introduced into Surrey, Norfolk, and elsewhere, with

Distribu-
tion.

Acclimati-
sation.

¹ A. Newton, "Dictionary of Birds," p. 388. London: A. and C. Black, 1893-1896.
VOL. I. 1 A

three exceptions. The first instance is that noticed by Professor Newton in his "Dictionary of Birds,"¹ when Baron Dickson succeeded in acclimatising the species near Gottenburg in Sweden; the second is that of its introduction in 1893-1894 to the Hohe Venn, a high tract of moorland on the borders of Belgium and Germany, south of Spa, where Red Grouse are still thriving; and the third the successful experiment on Lord Iveagh's property at Icklingham in Suffolk in 1903, where the birds, despite the necessity of an artificial water supply on the dry, sandy heaths, had increased in 1909, and appeared likely in 1910 to form a permanent colony. In the Hohe Venn district after two failures fifty pairs or more were liberated in August 1894, and by 1901 had increased to about a thousand head in spite of regular shooting. Professor Somerville of Oxford, who has kindly furnished particulars, saw the birds there in September 1910.

During the last twenty years it has been strongly borne in upon the general public, as well as sportsmen, that the welfare of the Grouse is an affair of national interest; for game of every description is becoming less and less a luxury of the rich, and more and more a regular factor of our food supply, facts which cannot be ignored by the modern economist, and are now considered to be well within the province of the Government, which has at last consented to bestir itself in the matter.

Here I propose to give a brief account of the position of the Red Grouse in the class of birds. In nearly all linear systems of classification put forward by modern systematists, whether they start from the highest or from the lowest forms of creation, the large order Galliformes—or its equivalent—stands about midway in the carinate or keel-breasted birds, being connected most closely on the one hand with the Falconiformes and Anseriformes, on the other with the Gruiformes and Charadriiformes. Its position is thus well ascertained, and no serious doubts have been raised as to its constituent members, except that the Tinamidæ (Tinamous) of South America, which have been sometimes included in it, are now by pretty general consent placed next to the Ratite birds, with keelless breastbone.

Under the order Galliformes may be placed in suborders the curious *Mesites* of Madagascar, the no less peculiar *Opisthocomus* or Hoatzin of northern South America, and the Old World *Turnices* (Button Quails) with their close ally *Pedionomus*; but the only suborder with which we are here concerned is that known by the name of Galli. Under the Galli, again, we need only make

¹ "Dictionary of Birds," p. 389.

passing reference to the group called by Huxley, Peristeropodes, where the toes are all in one plane; this includes the families Megapodiidæ or Mound-Builders of the eastern tropics, and the Cracidæ or Curassows of the neotropical countries. Huxley's second group, the Alektoropodes, with an elevated hind toe, is equivalent to the family Phasianidæ, which may be subdivided into the subfamilies Numidinæ, or Guinea-fowls, of Africa, the Meleagrinnæ, or Turkeys, of America, the Odontophorinæ, or "American Partridges," the Phasianinæ, or Pheasant, Partridge, and Fowl alliance of the Old World, and the Tetraoninæ, or Grouse. The last-named might well be classed as a separate family Tetraonidæ, were it not for the great difficulty of placing correctly such forms as *Caccabis* (Red-legged Partridge), *Francolinus* (Francolin), and *Coturnix* (Quail), which are so nearly allied to both Partridges and Grouse that we may even doubt the advisability of allowing a separate subfamily Tetraoninæ at all.

Grouse, as thus limited, are entirely confined to the Holarctic region, the great majority of the species being inhabitants of the New World, though a fair number, including the fine Capercailzie, the Black Grouse and the Hazel Grouse, are to be found in various parts of the Old World. Distribu-
tion.

The Red Grouse of Britain belongs to *Lagopus*, the only genus of Grouse common to both hemispheres, in which even the digits are feathered. This contains six well-defined species: the Spitsbergen Ptarmigan (*L. hemileucurus*) and the Rocky Mountain Ptarmigan (*L. leucurus*)—only found in the regions after which they are named—the Ptarmigan of Scotland and the mountains of the Palæarctic area (*L. mutus*), the "Iceland" Ptarmigan of that island, Greenland and the lower grounds of Northern Siberia and Arctic America (*L. rupestris*), the Willow Grouse of the north of Europe, Asia, and America (*L. albus*), and the British bird (*L. scoticus*)—with which alone we are concerned—indigenous in no other country.

All the forms of the genus *Lagopus* are anatomically identical, but the Red Grouse differs from the remaining members in that it does not turn white in winter. It has been thought to be merely the local representative of the Willow Grouse in Britain, though it differs from that species even in Variation. its summer plumage, and never possesses white wing-quills. It varies considerably in coloration, as will be seen from the following quotation from "The Cambridge Natural History." "The male in both summer and winter is more or less chestnut-brown above, with black markings and a reddish head; the lower parts are similar, but are usually spotted with white. In autumn the brown of

the upper parts becomes buff, and the lower surface is barred with buff and black. Mr Ogilvie-Grant recognises three types of plumage in the male, a red form with no white spots, from Ireland and Western Scotland; a blackish variety comparatively rarely found; and another largely spotted with white below or even above. Intermediate specimens constitute the bulk of our birds. The female exhibits, moreover, a buff-spotted and a buff-barred form; but in summer she is typically black above with concentric buff markings, and buff below with black bars. Her autumn plumage, which continues throughout the winter, is black, spotted with buff and barred with rufous.”¹ As we write, Mr Ogilvie-Grant has published in the “Bulletin of the British Ornithologists’ Club”² an elaborate account of the changes of plumage undergone by the Red Grouse, and of the points wherein he differs from Mr Millais and Dr Wilson; but this is not the place to enter into controversial matters, and our readers must form their own opinions on the subject.³ Various reasons have been suggested for the absence of a white winter plumage in the British bird, for which reference may be made to the late Professor Newton’s “Dictionary of Birds.”⁴

The Red Grouse is not polygamous; the birds pair very early in the year, and consequently breed at a time when the eggs are apt to be seriously damaged by late frosts, while the young often suffer from similar causes. The
 Habits. usual haunts are moors clothed with heather (*Erica*) and ling (*Calluna*), but in some parts at least of the north-west of England they are to be found on hills covered with crowberry (*Empetrum*), rush (*Juncus*), and other vegetation, where little if any heather or ling grows. As a rule, the nest is a slight structure of bents and so forth, placed in thick heather or grass, or even on almost bare ground; the eggs, ranging from five or six to more than a dozen in number, have a yellowish or buffish white ground-colour, normally blotched and spotted with reddish or blackish brown. The colour of the markings, however, varies considerably; in some specimens they are purplish or very rich red, in others orange-red. The eggs measure nearly 2 inches by rather more than 1. The cock utters his well-known crow at all seasons; the hen has a somewhat different note in the mating season, and when in charge of the young. The cock has also a clear ringing cry.

The general habits will be dealt with in the later chapters.

¹ “Cambridge Natural History,” vol. ix., *Birds*, p. 338. Cambridge, 1899.

² “British Ornithologist’s Club,” vol. xxii. p. 122. London, 1910.

³ *Vide* also chap. iii.

⁴ “Dictionary of Birds,” p. 391.

CHAPTER II

THE LIFE HISTORY OF THE GROUSE

By A. S. Leslie

No precise date can be given at which Grouse begin to pair, for this depends more upon the climatic conditions than upon anything else. In a mild winter Grouse will pair as early as December or January; but if, after they are paired, the weather becomes rough and stormy they will again congregate in packs, even after the usual date of nesting has arrived. Pairing.

The time at which they select their nesting ground (March and April) is also, to a limited extent, influenced by climatic conditions. On high moors, where the snow lies in late seasons till far into the spring, it sometimes happens that during the whole winter, and even up to the month of April, there is hardly a bird upon the hill, the whole stock being congregated on the lower-lying moors where there is "black ground" on which food can be obtained. In such seasons it is interesting to observe the return of the stock to the higher parts as soon as the snow begins to melt. As a rule the birds do not pair upon the low ground, but congregate in packs upon the edge of the snow, waiting for an opportunity of returning to breed on their native hill. A good example of this was furnished in the spring of 1908 on a high-lying moor in Inverness-shire. During the preceding winter there had been a heavy fall of snow which lay for many months on the higher ranges, and drove the Grouse down in vast numbers to the lower levels. On the moor referred to there was not a Grouse to be seen until the snow began to melt about the end of April. But at the first sign of thaw the stock began to return, and as each patch of bare ground came into sight a pair of birds arrived as if guided by instinct and commenced to nest. This year the shooting season turned out to be a record one, for upwards of

Pairing
sometimes
postponed
by snow.

five thousand brace were killed upon an area of 20,000 acres, and many more might have been shot without unduly reducing the stock.

While heavy snow during the winter may do little harm though it lies till far into the spring, a loss of stock may result where the fall occurs after the birds have returned to their nesting ground on the higher ranges. This occurred on a moor in Ross-shire in the year 1909, when a correspondent of the Committee reports as follows: "A heavy snowfall on April 24th put all the birds down to 'black ground.' They never went back to nest, and consequently the high ground, *i.e.*, over 500 ft., was a failure, and the low ground better than usual." Again, a correspondent in West Perthshire writes:—"In spring, when the breeding season is approaching a heavy snowstorm of some duration has on several occasions caused a most serious loss of stock, amounting to as much as half or more of the whole number of birds. After such a spring snowstorm and migration, large numbers of Grouse undoubtedly remain to breed on low and favourable moors within, say, ten or fifteen miles. These low moors are very heavily shot every year, but there is a constant migration of Grouse to them, both from overstocked moors, and from the high moors affected by snow." This is corroborated by a correspondent in the south of Scotland, who says: "I have an idea that if birds are forced to leave their usual ground (in spring), through deep untrodden snow, a good number may remain away and not return to their former ground."

Effect of
snow on
stock.

The subject of migration is more fully dealt with in another chapter.¹

During the mating season the pugnacity of the cock Grouse is well known, and in captivity the cocks have to be kept separate at this period, or disaster will certainly occur. Under natural conditions the fights seldom end fatally; but it is certain that the presence of a quarrelsome cock-bird in search of a mate seriously interferes with the pairing of the other birds in the vicinity. Observation in the field goes to prove that old cocks are more pugnacious than young ones, and as they are less valuable for breeding purposes the object of every moor-owner is to reduce the number of old cocks by every means in his power.

The nest, a slight hollow scratched in the ground and lined with a scanty layer of grass, heather, etc., is usually placed on the sunny side of a tuft of heather, and preference as regards its site seems to be given to an area on which the heather is moderately well grown rather than where it is

Pugnacity
of cocks.

¹ See chap. xxiv.

rank. Birds will always nest in a place where they can see all round, if possible, hence their avoidance of long heather.¹

Nesting.

Dry ground is always preferred; birds will not nest on boggy or damp ground, and are more likely to leave their nests on account of wet than for any other reason.

On some moors where the heather has been very closely burnt or the stock is unusually large, the Grouse appear to be unable to find nesting ground exactly suited to their requirements, and on these occasions they will boldly depart from their usual habits and will nest in short heather, flat dead bracken, or even on a bare unsheltered piece of burnt ground, leaving the nest as open as that of the Lapwing. It is important to note that in all cases open sites devoid of all covering are preferred to really long overgrown heather.

The time of nesting varies according to the season and the latitude. As a rule, most of the eggs are laid by the latter end of April and the beginning of May; but a case has been reported of eggs being found as early as March 28th, and the Rev. W. B. Daniel records that "on the 5th of March, 1794, the Gamekeeper of Mr Lister (now Lord Ribblesdale), of Gisburne Park, discovered on the Manor of *Twitten*, near *Pendle Hill*, a brood of Red Grouse seemingly about ten days old, which could fly about as many yards at a time. This was an occurrence never known to have happened before so *early* in the year."² Macdonald states that the hen begins to lay at the end of March,³ while Macpherson, writing in the *Fur and Feather Series*, says that "In the Island of Skye April 24th is a decidedly early date for a full clutch of Grouse eggs."⁴ It is an interesting fact that, from the evidence obtained from many moors, of varying altitudes ranging from the south of Wales to the north of Sutherland, there is a difference of only two or three days in the dates when the earliest eggs are found; March 30th in Yorkshire and Perthshire, and April 1st on high moors in Inverness and Sutherland are dates frequently recorded for the first nest. The date at which the first clutch is completed varies by a full fortnight on high and low ground and on north

¹ Macdonald in "Grouse Disease" makes the following statement: "The happiest condition in which a nest can be found is in growing heather of about a foot in length, and in the immediate proximity of short young heather." (Macdonald, "Grouse Disease," p. 23. London: W. H. Allen & Co., Ltd., 1883.) And in another place he writes: "Grouse never nest amongst old, rough heather, always in a little tuft at the side or among the bent." (*Ibid.*, p. 26). Macpherson in the *Fur and Feather Series*, states that "It is a fallacy to suppose that Grouse like to nest in *very* old heather." (*Fur and Feather Series*, "The Grouse," p. 22. London: Longmans, Green & Co., 1894.)

² Daniel, "Rural Sports," vol. iii. p. 108. London: Longmans, 1812.

³ "Grouse Disease," p. 99.

⁴ *Fur and Feather Series*, "The Grouse," p. 21.

country and south country moors. In Yorkshire by the end of April many birds have begun to sit, while in central Scotland from April 25th to May 20th would probably cover the dates by which the full clutches are complete on most moors. The intervals between the laying of each egg vary enormously in captivity, probably also in nature, depending upon the weather; for example, at the Committee's observation area in Surrey it was noted that one hen took twenty-nine days to lay ten eggs—an average of one egg every three days; another laid only four eggs in twenty-six days, or an average of one egg every six and a half days. The clutch averages from seven to ten, and rarely reaches twelve.

Macdonald states that the hen lays eight to fourteen or sixteen eggs,¹ while Macpherson gives seven and eight as the most usual number of eggs, and states that "more than ten is quite exceptional."² Seebohm, who speaks with authority on all questions of British oology, states that the number of eggs laid would seem "to vary with the propitiousness or otherwise of the season. In very wet and cold springs the smallest clutches contain four or five, and the largest eight or nine; whilst in very favourable seasons the small clutches are six or seven, and the larger ones from ten to twelve, or even fifteen and seventeen; but in the latter cases it is probable that the eggs may not all be the produce of one bird. In an average year most nests will contain seven or eight eggs. Birds which breed late on the high grounds do not seem to lay fewer eggs than those which breed early in the more sheltered situations."³ A correspondent of the Committee in Forfarshire has reported a case of two Grouse hens sitting side by side—each on six eggs in a double nest; and the field observer has seen two hens sitting on one nest with twelve eggs.

For the following descriptive notes on the eggs of the Red Grouse in his "Birds of Europe," Dresser states that he is indebted to Seebohm: "The ground colour of the eggs of the Grouse is usually a pale olive, spotted and blotched all over with dark red-brown. The spots are frequently so confluent as almost entirely to conceal the ground colour. In fresh-laid eggs the brown is often very red, in some instances almost approaching crimson. It appears to darken as it thoroughly dries, and sometimes almost approaches black. When fresh laid the colour is not very fast, and before the eggs are hatched the beauty of the original colouring is generally very much lessened by large spots

¹ Macdonald, "Grouse Disease," p. 99.

² Fur and Feather Series, "The Grouse," p. 22.

³ Seebohm, "British Birds," vol. ii. p. 430. London: R. H. Porter, 1885.

coming off altogether, no doubt from the friction of the feathers of the bird when sitting. If the weather is wet when the bird begins to sit this is much more the case. When the colour has once become thoroughly dry it will bear washing in water without injury.”¹ In his most recent work Mr Dresser adds: “When blown and kept for some time, the ground colour fades to buffy white, and the spots and blotches darken in some cases to blackest brown. Those in (Mr Dresser’s) collection measure from 1.60 by 1.14 to 1.82 by 1.32 inches. Mr Jourdain gives the average measurement of thirty-six eggs as 45.56 by 31.8 mm., and the average weight of eight eggs as 1.845 g.”²

There is no truth in the belief that disease will follow if the eggs are not well coloured. Very often the uncoloured part of the egg whitens at the same time as the coloured part fades or is washed off, thus making an egg of “bad colour.”

It is interesting to note that a bird of five years old lays fewer eggs and of a smaller size than a bird of one or two years old.

The net yield of the nesting season greatly depends upon the weather in spring; frost before sitting, snow after hatching, heavy rain following a drought when the birds have nested in low-lying ground liable to submersion, are some of the principal dangers to which early broods are exposed. The eggs also may be lost by a long spell of wet weather, even up to the point of hatching. This is probably not a matter of common occurrence, but in the spring of 1906 the Committee’s field observer saw nest after nest deserted owing to rain. The nests on the low ground fared worst; in some the eggs did not hatch at all, in others only one half, or even fewer, were productive.

Effect
of bad
weather on
eggs and
young.

The parent birds seem to defy the elements at all times, and during the period of incubation the hen will continue to sit upon her eggs apparently oblivious of the fact that a snowstorm is raging which has driven every other living creature off the moor. During such a storm hens are completely covered with snow as they sit upon the nest, for in hard weather instinct teaches them not to desert the post of duty. Observation of the bird at these times is difficult, for even the most enthusiastic naturalist is not often tempted to explore the higher ranges of the ground in the face of a blinding blizzard. We must to some extent form our conclusions by observation

Nesting in
snow.

¹ Dresser, “Birds of Europe,” vol. vii. p. 170. London: published by the author 1871-1881.

² Dresser’s “Eggs of the Birds of Europe,” p. 623, Pl. LXVII., Fig. 1. London: published for the author at the Office of the Royal Society for the Protection of Birds, 3 Hanover Square, 1905-1910.

of after-results, and certainly there is little doubt that the effect of a heavy snowfall, while the birds are sitting, does not appear to produce the number of unhatched clutches of weather-bleached eggs which might be expected. Sometimes, no doubt, matters reach the limit of endurance when, urged by the pangs of hunger, the hen is forced to wander away in search of food and grit, and on her return finds all trace of her nest buried beneath a smooth, white drift. Even in this case all is not lost; the snow fortunately does not lie long in the months of April and May, and in due time she recovers her nest and resumes her domestic duties. It is recorded that in 1908, on a Midlothian moor, a heavy snowfall during laying-time covered the nests to a depth of 9 inches for a period of ten days; many eggs were lost, some even being laid on the top of the snow; in many cases the hen bird returned to her nest after the snow had gone and laid more eggs beside those which had been covered—some of these birds hatched out every egg. Other cases have been reported where the eggs were covered with snow for so long that their colouring matter had disappeared, and yet they produced a healthy brood.

From observations made upon Grouse in captivity it appears that during the period of incubation the hen will often leave her nest for several days at a time, for no apparent reason, and will return again and hatch out the whole clutch—this power of absenting herself without disaster to her eggs must under natural conditions stand her in good stead when the severity of the weather makes the task of incubation unendurable; but it is only in the earlier part of the sitting season that her absence is unattended with risk, for once circulation has commenced in the embryo chick the eggs must not be allowed to become cold. Only when the hen is forced to leave the nest on account of heavy rain is there a danger of her deserting the nest permanently—three days of incessant wet will suffice for this.

Another danger to which the eggs of Grouse are liable is that of being destroyed by frost while the hen bird is off the nest. This danger is greatest during the period before the full clutch has been laid, for after incubation has commenced the hen will not readily leave her nest during frosty weather for any length of time. Before the hen commences to sit she will often cover up the eggs in the nest with twigs of heather, grass and bracken, and this must save many of them from the effects of frost.

The Committee has had an exceptionally good opportunity of studying the effects of frost upon the eggs in the spring of 1908, when an extremely severe

frost was reported from every district of England, Scotland and Wales. For three days in the third week of April the thermometer registered from 10 to 27 degrees Fahrenheit. The Committee requested its local correspondents to make careful observations on the resulting damage, and the replies received are given in the form of an appendix.¹ Several interesting facts were brought to light—in general it was stated that the effects of the frost had been disastrous; but when the evidence came to be analysed the proof seemed strangely incomplete, for very few reporters were able to state from personal observations that eggs laid before the frost had failed to hatch. On the other hand, several accurate observers reported that they had marked down eggs so frozen into the materials of the nest that it was not possible to lift them out or to separate them from each other, yet it was afterwards found that these eggs hatched out healthy chicks. On April 13th six Grouse eggs were found in a nest amongst heather when the temperature was 25 degrees of frost—and all six hatched out. On another occasion, when it happened that some Pheasant's eggs had been laid in a Grouse's nest, the Pheasant's eggs were the eggs which failed, while the Grouse's eggs were successfully hatched. Many correspondents went so far as to say that unless the frost was sufficiently severe to split the egg there was no danger of their fertility being affected, and of very many gamekeepers to whom the question was put very few could state that they had actually seen a Grouse's egg split by frost.

Actual splitting of the eggs by frost does occur, but is exceedingly rare when the nest is in its customary position in heather. When placed in the open probably the eggs are liable to suffer just as Plover's eggs did in 1908, and an extra hard frost will sometimes split them. Even very scanty heather-growth retains the warmer air, and so shelters the nest and eggs from frost and winds. Moreover, if sitting has not begun the eggs are generally more or less buried in the material of the nest, so much so that it is impossible to count them unless they are disturbed.

Enough has been said to emphasise the statement that the eggs of the Grouse are wonderfully tolerant of adverse weather conditions; the fact is not sufficiently well recognised, and because occasional losses occur there is a tendency among gamekeepers to put down every failure of stock to some sharp frost or heavy snowfall in the month of April or May. They often do not inquire whether as a matter of fact any eggs were laid at the date when the frost occurred, they

¹ *Vide* vol. ii. Appendix I.

seldom support their statement by pointing out nests deserted by the hen after being buried in the snow, they keep the plausible explanation ready for use if required, and if the stock after all proves to be up to the average, they feel secretly rather surprised, but say nothing about the adverse conditions in the breeding season, for the excuse may be required the following spring. Thus much valuable evidence is lost owing to the very natural desire of the gamekeeper to prove himself the innocent victim of circumstances.

Obviously, if the occasional snowstorms and moderate frosts of a normal April were really responsible for the damage so often attributed to them, it would follow that in a really inclement nesting season, such as occurred in 1908, the effects would have been disastrous throughout the length and breadth of the country. As a matter of fact, the bags in the autumn of that year, though unequal, were well up to, and in some places far above the average; and even where a shortage of birds was reported the failure could often be traced to other causes than the unfavourable weather-conditions in the spring.

While the evidence collected does not confirm the view that snow and frost in the nesting season are extensively destructive to the eggs of Grouse, there is some reason to believe that unfavourable weather, occurring immediately before the date of laying, has an injurious effect upon the breeding powers of the parent birds. In the spring of 1908, for example, it was observed that on many moors birds which had paired, and were about to nest, became packed again on the arrival of frost and snow, and postponed their breeding operations until some time after the return of favourable conditions. The result was that they nested several weeks later than they would otherwise have done, and not only were their broods late, but the number of eggs laid was smaller than usual—sometimes averaging only four and five in a nest. The resulting smallness of the coveys was often accounted for by the hypothesis that several eggs in each nest had been destroyed by the frost in April; but there was little direct evidence of this, and it seems equally reasonable to suppose that the power of egg production had been impaired by the enforced postponement of nesting. The data are insufficient to establish this theory, but the point is worthy of a passing mention.

It is certain that some of the eggs were lost owing to their having been dropped on the snow and not in a nest at all. After a certain stage of development the egg is laid wherever the bird happens to be. It is not uncommon to find eggs dropped in this accidental manner lying on the ground or on snow.

Interrup-
tion of
breeding
by bad
weather.

During the nesting season the hen leaves her nest for a short time in the morning and evening to feed and drink, and her presence in any particular part of a moor may be known by the large "clocker" droppings peculiar to a sitting bird.

During the period of sitting the Grouse seems to be able to intermit its natural odour, and thus escape the notice of dogs and vermin. This point is noted by St John in "Wild Sports of the Highlands" when he states: "It is a curious fact, but one which I have often observed, that dogs frequently pass close to the nests of Grouse, Partridges and other game without scenting the hen bird as she sits on her eggs."¹ Probably the cause of the loss of scent is that when the bird is sitting still the air does not get amongst the feathers and so the scent is retained. The same remark probably accounts for the fact that at midday, when the birds are resting, they are very difficult to find with dogs.

The young Grouse are hatched after an incubation of twenty - three to twenty-four days, and leave the nest soon after they are freed from the shell. They are anxiously guarded by the parents, the hen being more attached to them than the cock, who, when they are disturbed, is the first to fly from danger, though it may be only for a short distance. The hen, on the other hand, will risk any danger rather than leave her brood—be it only a single chicken or two. Often, too, like the Partridge and many other birds, she will feign a broken wing and flutter over the heather, apparently in a terribly damaged condition, until she has lured the intruder away from her brood. This fluttering action of the old bird should always be taken as a warning that the brood is young, that the squatting chicks are probably invisible, and that the danger of treading on them is great. It is most inadvisable to allow people who have flushed a cock or hen to walk about to see the size of a brood.

It is at this stage that the weather conditions become important, for the young chicks are liable to many dangers. It is true that they do not suffer from the cold, drizzly, sunless weather which destroys so many coveys of young Partridges, they are too hardy for that; but heavy snow, hail, or rain often takes its toll and leaves little trace behind beyond the fact that the coveys are found to be reduced in numbers when they come to the gun. Probably the half-grown chick runs more risk from weather

Loss of
scent while
sitting.

Hatching.

Weather.
conditions
harmful to
young
Grouse.

¹ St John, "Wild Sports and Natural History of the Highlands," p. 29. London: John Murray, 1878.

than when it is newly hatched, for its size prevents it from being completely covered by the hen when cold weather or heavy rain sets in.

The period immediately following hatching, though so critical, is the period regarding which least is known. Few keepers like to disturb the ground at this time, and so the young bird's battle for life is fought unobserved, and only the closest and most patient observation would reveal the true conditions under which the chick's existence is passed.

The young Grouse, even although they may be squatting within a few feet of the observer, are very difficult to find; they seem to have the power of making themselves invisible at will, as they cunningly crouch by the side of a tuft of grass or heather, which often matches in colour the yellow, brown, and chestnut mottled down that covers their little bodies for the first few weeks. When at last a chick is discovered and lifted up in the hand its first "cheep" is the signal for the others to scuttle away out of their places of concealment, or, if they are upwards of a month old, to make their effort at escape by a short flight, after which they are apparently incapable of a second attempt.

It is astonishing how little accurate knowledge we have of the principal dangers to which the young Grouse is exposed.

The practical gamekeeper admits that many dangers exist, and without weighing them too closely in the balance he does all he can to mitigate each of them. He knows, however, that in spite of his care there must be a certain percentage of losses from one cause or another, and it is with some anxiety that he proceeds to the moor towards the end of July to inspect the condition of the stock. The result is sometimes unexpected, often he finds the birds have safely survived the perils of youth, and that the moor is well stocked with unbroken coveys; at other times he is perplexed to discover that the well-filled nests and successful hatchings are represented by a few ragged broods of two or three birds, and a large number of barren pairs. He endeavours to account for the disappearance of the young birds, and in his search for a reason he eventually hits upon something which has some appearance of plausibility, and frequent repetition soon places theory in the realm of established fact.

Migration is one of the commonest theories, and is supported by the fact that few, if any, dead bodies are found on the ground. The migration doctrine presents some difficulties, for the Grouse in its earlier stages is not by nature a wanderer, and a brood is usually found, at all events

up to the end of July, not very far from where it was hatched out. Then, again, it is difficult to explain how on a large moor the young birds have departed before they are capable of sustained flight, especially if none of the neighbouring moors have received any noticeable addition to their stock. Lastly, it is permissible to ask how is it that when the young birds emigrated to more congenial surroundings they omitted to take their parents with them? Each of these points presents a difficulty, and the combination of them renders the migration theory untenable as an explanation for the absence of birds at any time up to the beginning of August.¹

Another favourite theory is that all the young birds have been drowned, and if it so happens that there has been a severe thunderstorm in June the theory becomes a certainty—though not a single drowned ^{Drowning.} chick may have been found on the moor.

There is no doubt that many young Grouse are destroyed by drowning, either as a result of being caught in a drain by a heavy shower, or by the flooding of low-lying ground. It is difficult to estimate the loss ^{Sheep drains.} occasioned by drowning in sheep drains, owing to the extreme difficulty of detecting the small corpses in the swollen stream. One of the Committee's correspondents, a gamekeeper, who makes it a rule to inspect all the drains upon his ground several times during the nesting season, states that on one occasion only has he found a drowned chick in a drain. This evidence is, of course, only negative, and against it has to be reckoned the fact that many observers have spoken definitely as to the damage arising from this cause. On many moors the sheep drains have been scoured by floods into deep chasms, from which it would be difficult for the chick to emerge on the approach of danger, and any one who has seen a hill drain immediately after heavy rain, when it is running bank high in a miniature torrent, can picture the risk which might attend any attempt on the part of the mother bird to lead her brood over the obstacle. Much may be done to minimise this risk by forming little backwaters in the drains with shelving banks, by which the young Grouse may escape in time of danger. With regard to flooding, it is necessary to speak with more reserve. Flooding is a gradual process, and the instinct of self-preservation, which teaches the young Grouse to ^{Flooding.} hide from his foes, will doubtless also teach him to retreat before the rising waters. In one case, however, flooding is a real menace, for if the

¹ *Vide* vol. ii. Appendix G.

nesting season is a dry one Grouse have been known to nest in very unsuitable places, such as the beds of burns and dried-up pools and water-courses—often with most disastrous results when the weather breaks.

But, if there has been no rain, the drowning theory must be discarded, and its place is taken by the drought theory; in other words, the fine, dry, warm, sunny weather which is credited with producing a healthy stock in a good year is the cause of their wholesale destruction in a bad year.

Nor do we know exactly what proportion of Grouse meet their fate from vermin; that a certain number are killed by foxes, ravens, hoodie crows, stoats, weasels, and even gulls, may be admitted; but when we come to apportion the blame we again find ourselves without sufficient evidence to amount to proof. The subject of vermin is dealt with more fully in another part of the Report.¹

Occasionally it is found that old birds as well as young have disappeared, and when this happens it is customary to ascribe the cause to "Grouse Disease." amongst the adult birds, for it is well known that if a parent bird dies from disease or any other cause there is little chance of her brood surviving.

At a very early stage of the Inquiry it became evident that the loss of young stock on a large scale had never hitherto been properly accounted for, and required further investigation by the Committee.

The Committee believe they can offer a solution of this problem. During their Inquiry into the causes of mortality in Grouse they discovered a certain unicellular intestinal parasite, one of the Protozoa, a Coccidium, known as *Eimeria avium*, which in certain cases is most destructive to the young chick, but is rarely fatal to the adult bird; this Coccidium is fully described in another chapter of this Report.² The discovery of the disease caused by this pathogenic organism and known as Coccidiosis justifies the view that when there has been extensive mortality amongst the young stock which cannot be accounted for in any other way, it is almost certain that the chicks have met their fate by this infantile complaint.³

Coccidiosis as a disease of game birds and poultry is now being rapidly recognised in this country, and the disease is also being investigated in America.

Still there remains the difficulty that the dead bodies are not found in

¹ Vide chap. xx. pp. 443 et seq.

² Vide chap. xi. pp. 235 et seq.

³ Vide also vol. ii. Appendix G.

any quantity; it must be remembered, however, that the infant Grouse is a small object, and any one who has searched in vain in the heather for a full-grown bird which has fallen to his gun can realise the difficulty of finding a tiny chick upon a moor where the whole stock does not average more than a bird to several acres. Coccidiosis chiefly attacks the birds when they are very small; the chicks die in the heather, the little carcasses are rarely found, and in a short time they disappear altogether for, even if they have not been devoured by vermin or removed by heat, wet, flies, maggots, or burying beetles, the small bones do not make lasting skeletons, and would not be discovered even if the moors were searched.

In spite of difficulties the field observer and other members of the Committee's scientific staff have by diligent search been able to find a certain number of small dead chicks on the moors; in almost every case the cause of death has been found to be Coccidiosis. Many other cases of Coccidiosis have been received for examination from various parts of Scotland and Yorkshire, and others have been obtained from the Committee's observation area in Surrey.

Fortunately it is only in exceptional cases that we have to consider the question of a wholesale disappearance of the young stock from pathogenic causes. Under normal circumstances the Providence that watches over all young things brings to maturity a large percentage of the birds that are hatched; but Providence may be assisted, and the methods by which it may be assisted are fully discussed in another part of this Report.¹ Suffice to say that in the earlier stages of the life of the Grouse the state of the moor is of great importance to the welfare of the birds. If the heather has been well burnt in a systematic manner the chicks have access to shelter in time of danger, yet are not lost in a wilderness of rank growth should a shepherd's dog scatter the brood in all directions; vermin is kept down, and, most important of all, there is easy access to a plentiful supply of suitable food in the strips or patches of heather which are available in various stages of growth.

Care of
the moor
in the
interests
of young
Grouse.

The place above all others where we may be sure of finding a brood of young chicks, if there are any on the ground, is amongst rushes and long grass in the more swampy parts of the moor; this is specially noticeable in very dry seasons. Whether the chicks seek these damp spots for the sake of shelter from the heat or in quest of insect life is not known.

¹ *Vide* chaps. xvii., xviii., xx.

Flies, spiders, beetles, and greenish caterpillars about $\frac{3}{4}$ -inch long, as well as slugs and chrysalides, have all been found in the crops of chicks. Fresh *Calluna* heather shoots, moss capsules, and tender blaeberry leaves just opened, if they are to be had, are also generally present; and as the young birds grow older heather becomes more and more their staple food.¹

In a chick of a few days old, where the food consisted of small caterpillars, there was no grit to be seen in the gizzard; and, in another, the muscles of that organ, with its toughened lining, seemed sufficient to crush the soft blaeberry shoots. But it is the rule to find even in the youngest chick's gizzard a certain small quantity of fine quartz-grit and sand.²

When half-grown the crops of those examined contained a large percentage of heather, and the gizzards contained about half the amount of grit that is usually found in old birds, but in smaller fragments.

Water, as supplied by streams and pools, does not appear to be necessary in the earlier stages where there is plenty of young heather; insects, the succulent juices of the young heather shoots, and dew seem to provide all the moisture necessary. Broods are often hatched out far from any stream or pool, and they can generally be found within a few yards of the same spot till they are able to fly. On this point, as it affects the hand-rearing of Grouse, a well-known moor-owner writes: "I have never noticed that the young Grouse, when half-grown or older, require more water than what they pick up in the grass in wet weather, and what is sprinkled on the grass or heather at meal times, in dry weather. Old Grouse go to drink two or three times a day at most; they seem to know how much is good for them; whilst young Grouse, if allowed access to water, are apt, or almost certain, to drink too much, and scour. This, of course, refers to tame birds." Another of the Committee's correspondents (a gamekeeper on a large moor in central Perthshire) says: "Regarding water, I have known several broods fetched out 600 yards from the nearest water of any kind, in a dry season; and they continued to thrive without water for at least three weeks after hatching."

As the Grouse grows older, the parent birds relax their anxiety for the brood when disturbed, and, although they lie very close, the hen bird no longer flutters along the ground endeavouring to distract attention.

Vide chap. iv. p. 73.

² *Ibid.*, p. 95.

Every keeper knows too well the danger that attends the needless disturbance of his beat at this time, especially in a high wind, which may carry the flushed birds hundreds of yards from their home. Instinct and the call of the parents may guide them back; but it is better that they should be kept quiet. It has been noticed that when a young brood are once upon the wing, in anything like a strong breeze, they appear to be unable to alight with safety; at the end of the flight they dash headlong into the heather, or on to the ground, and frequently come to an untimely end.

Disturb-
ance of the
moor un-
desirable.

With the arrival of August 12th the Grouse comes into the glare of publicity, and there is little relating to his life history between this date and the end of the shooting season that is not known to the average sportsman; but even so there are variations in their habits in different localities which still remain a mystery, and it may be worth while to mention some of these.

Grouse in
the shoot-
ing season.

While in the majority of cases the birds appear to be wild in proportion to their growth, this does not seem to be the only factor in the case, for in some districts on the west coast, notably in Skye, Grouse will sit close throughout the shooting season. It has been said that the reason for this is that in the districts in question birds of prey survive in larger numbers than elsewhere, and that the Grouse has not lost its instincts of self-preservation against the attack of its natural enemies. This may be true, but is not altogether convincing, for it is well known that to sit close is no protection against the Eagle, though it may be against the Falcon. The Grouse instinctively knows this, and the appearance of an Eagle, or even a Heron, is the signal for all those on the alert to fly in terror to some distant place of safety.

Grouse feed off and on throughout the day; but it is only in the evening that the crop retains the food which is then required for use during the night.

Feeding
habits of
Grouse.

It is often stated that Grouse feed only in the evening, but the observations of the Committee make it quite clear that this is not the case. It may be observed in passing that at midday the Grouse appear to feed less, and towards evening far more than at any other time. Midday is given up to rest, and, in summer, to shelter from the heat of the sun, and the evening devoted to the complete filling of the crop with food for digestion during the night. Colquhoun in "The Moor and the Loch" refers to this habit as follows: "In sultry weather they lie quite still except at feeding time, and not

having stirred perhaps for hours the dogs may come within a yard or two before winding them.”¹

In the early part of the day and at dusk Grouse are found looking for grit, on the rough moor roads and tracks, or along the burn-sides, where every fresh spate washes down a new supply.

The attraction presented to the Grouse by a suitable supply of grit is most marked. Good grit is to the Grouse what raisins are to Pheasants, and salt to Deer. They often fly long distances to obtain it, and in districts where Grit.

it is scarce they will congregate in numbers along the railways and roads that traverse the moor, in order to avail themselves of the supply thus artificially introduced.

Towards midday Grouse are generally found on the “tops” and higher grounds, and especially amongst broken moss-hags; or, if the weather is very hot, they may be flushed from the burn-sides and shaded places; in very rough weather they do not scorn the shelter afforded by a ledge of rock or bank of peat, and may then be best approached down wind. The best shooting is often got late in the afternoon on the low ground, to which the Grouse have descended to feed before “jugging,” with crops crammed with heather shoots.

When moving from one part of a moor to another Grouse usually fly low, and as their principal time for shifting their ground is in the early morning or at dusk they run a serious risk of death by collision with the wire sheep fences so common on many moors.

This danger can be to a great extent averted by having all wire fences carefully “bushed” with bits of brushwood. Small branches of larch are best for this purpose, as they can be easily turned into the wires, and do not readily blow out—a fair-sized branch every 5 yards is sufficient. Spruce branches are also used. Telegraph wires are not so common on a moor as fences, and not nearly so dangerous, while the cost of protecting the birds from them by game-guards makes it hardly worth while to consider them.

The Grouse, like the Domestic Fowl, the Pheasant, and the Partridge, is a “dusting” bird, and wherever a peaty or sandy bank has a sunny exposure a “scrape,” with a feather or two half embedded in the soil, is to be seen. The fine particles of impalpable dust, by getting into the breathing apertures of the troublesome insects which are found on the birds, afford the latter temporary

¹ Colquhoun, “The Moor and the Loch,” p. 184. 6th Edition. Edinburgh: William Blackwood & Sons, 1884.

relief. Grouse also like to sun themselves on a warm bank or slab of rock—often resting with one wing extended.

The practice of “becking” has been thus described in a note by Mr Alston in Dresser’s “Birds of Europe”¹: “Early on frosty mornings the cocks are fond of perching on a knowe or hillock and uttering their clear-ringing *er-eck*, *kek-kek!* *wuk, wuk, wuk*. At such times they may often be seen to rise perpendicularly in the air to a height of several feet, and then drop again on the same spot.” “Becking” is fully described by the Rev. H. A. Macpherson in the Fur and Feather Series, where it is pointed out that the practice is in the nature of an amorous demonstration by the cock Grouse with the object of attracting his mate,² and it may be compared to the peculiar antics adopted by the Blackcock and Capercailzie from a similar motive. “Becking,” however, is not confined to the breeding season, indeed it is more usual during the autumn and winter months than in the spring. Mr Macpherson describes in a most interesting chapter the manner in which Grouse may be shot by taking advantage of this peculiar habit.

Grouse, when fully grown, do not pass the night huddled together like Partridges, but “jug” singly amongst the heather, taking care not to be far apart. From the traces left in time of snow it is found that they usually lie about a foot or two apart, so that a pack of a hundred may be contained within an area of a dozen square yards.

In the words of a Highland gamekeeper: “Grouse glory in their ‘hardiness,’” and it is almost incredible how little they are affected by wet, cold, and snow. It may indeed be said that so far as the adult Grouse is concerned it matters not what the weather is so long as his food supply is not affected. They will never desert high ground for low ground merely on account of a heavy fall of snow, provided that there is sufficient wind to keep the exposed ridges clear, and thus give access to the heather; and even if the whole moor should be covered they will burrow in the soft snow to reach the heather underneath. It is quite common to come upon birds in holes a foot or two under the loose snow. It is only when the snow has become covered with a hard, icy crust that the Grouse begin to feel the pinch of hunger. On these occasions they may be seen in large packs following in the track of a herd of deer or a flock of sheep in order to take advantage of the broken surface. They

¹ “Birds of Europe,” vol. vii. p. 168.

Fur and Feather Series, “The Grouse,” pp. 65-72.

have even been known to eat the old unburnt stick heather which on all other occasions they reject as unfit for food; but this is probably the last resource of the famine-stricken stock, and hardly justifies the practice of leaving a large amount of this unwholesome old heather as a food reserve in time of snow, for such a practice must greatly reduce the available supply of food at the critical period of early spring. A better practice is undoubtedly to burn all the more exposed ridges and knolls with careful discrimination, so that in whichever direction the snow may drift there is a good chance that some good feeding heather will be left bare.

It might be thought that where a heavy snowstorm occurs during the night there would be a risk of whole packs of Grouse being covered up and smothered by the drifts as the birds were jugging in a sheltered hollow. Sheep are often lost in large numbers by such misadventure, but Grouse never, for as they jug in the lee of a peat-hag or a moorland dyke they tread the snow under them as it falls, and are found next morning safely collected on the surface, though their fresh droppings several feet below show the level at which they began their night's repose.

It has been said that Grouse often avail themselves of the shelter of woods and plantations in time of snow; but the evidence on the subject is most contradictory. In some districts it has been found beneficial to plant trees as a shelter for Grouse; in other districts, especially in the north of Scotland, they never use woods for shelter.

It is generally believed that a hard winter with much snow is beneficial to the health of the stock in the following spring, and the reason commonly given is that the hard weather kills off the weaklings. There is no evidence to support this theory. Grouse are seldom found dead during the winter months, and when they are the cause can never be ascribed directly to the effects of weather. If the belief that snow is beneficial is well founded, some other reason must be sought; perhaps the fact that the weather has caused the stock to shift, and so introduced new blood where required, may have something to do with the improvement: more likely, however, the solution is found to be connected with the question of food supply. Ground which has been covered by snow for a period of several months provides better and more wholesome food than ground which has been heavily stocked, for when birds return in the spring they find the food supply still untouched by Grouse or Sheep, and the fact that it has been out of reach for so long has prevented it from being so heavily infected by the larvæ

of *Trichostongylus* as the lower moors which were crowded with Grouse throughout the winter. The melting of the snow may also have the effect of washing the Strongyle larvæ out of the heather.

If the birds are well matured by August 12th they often begin to "pack" after the first few days' shooting, and will not then readily lie to dogs. Packing may at times take place so early as to make shooting over dogs an impossibility. On this account the poor results formerly obtained on most English moors led to the introduction of "driving." In Caithness and some other districts the Grouse, being more backward, do not pack except under exceptional conditions.

This custom of packing is worthy of study, for it may be found to have a direct bearing upon the questions of disease, migration, interbreeding, and the preservation of the stock.

In the first place, it may be stated that it is the young birds rather than the old birds that tend to form into packs in the earlier months of autumn, though the older birds will follow suit as the winter advances. Consequently, when packing first begins, it is the older birds that suffer the greatest loss in a day's Grouse driving, for they come up to the line of butts in twos and threes, and are "mopped up" to a bird, whereas the larger packs of younger birds merely yield a percentage of their numbers to swell the bag. To this cause may perhaps be ascribed some of the beneficial results which attend the introduction of driving on many moors.

Another important fact connected with packing is the tendency of the stock to separate into sexes—there are hen packs and cock packs, or at least each pack contains a large majority of one sex. It has been noted that certain hills in a range of moorland are frequented by hen packs, others by cock packs.

The normal time for packing is the autumn and winter months, and the more severe the weather the more marked is the tendency of the birds to form into large companies and flocks. Hens pack more readily than cocks; the old cock does not appear to be of a sociable disposition, and often throughout the winter he will remain in solitary state, and only join the pack temporarily during a period of unusual storm. This tendency is often taken advantage of by those moor-owners who regard the old cocks as a menace to the health of their stock, and on many well-managed moors a rigorous crusade is carried on against the old single birds that frequent the bare tops, while their younger relatives occupy the lower ridges.

During the winter months the advent of mild weather will often break up the packs for a while, and many cases have been reported of birds being scattered over the moor in pairs even in the months of November, December and January ; but with the return of wintry conditions their gregarious habits assert themselves even up to the commencement of the nesting season.

The reason why Grouse should pack in winter has often been discussed. The most favourite explanation is that they combine with a view to obtaining food in time of scarcity. Another theory is that, like many other birds and animals, the natural instinct of the Grouse is to congregate in flocks, and that this instinct is only departed from to meet the requirements of the breeding season. It is probable that various motives induce the birds to congregate in packs. Some of these motives may be briefly mentioned. (a) To get on to the high bare tops out of the wet—it is observed that Grouse are always more packed after wet weather. (b) To go down to feed on the cornfields ; Grouse are seldom found feeding singly on the stooks ; this may be due to the natural timidity of the wild bird, which makes it fear to resort to the unwonted feeding-ground unless supported by numbers. The same rule applies with even greater force to the case of birds leaving their own ground and wandering far afield in search of food ; such migrations never take place except in large packs. (c) Owing probably to the same cause, Grouse invariably tend to pack after they have been much disturbed, especially by driving, on moors which for some reason have not been shot over for a season ; the birds do not pack until late in the year. (d) In dry weather small packs of two or three coveys are found at or near the springs even on August 12th.

Undoubtedly, the most common cause of packing is scarcity of food. It has already been remarked that during the winter months the feeding area on every moor is restricted to those parts where the heather is of such a character as to resist the effects of frost and cold ; hence the birds tend to concentrate upon these food centres.

The habit of packing is probably indirectly connected with the question of disease. If we admit that the congestion of a large number of birds upon small areas of moor is conducive to the deposit in dangerous numbers of the larval worms which cause disease on the favourite feeding-grounds of the birds, then it follows that the pack formation is in itself a danger to the health of the stock. This view is supported by the fact that where packing is the exception rather than the rule, as in the west coast of Scotland, disease

is of rare occurrence. It is obviously impracticable to induce the Grouse to change this dangerous practice of congregating in packs; but in another part of the Report suggestions are offered for minimising the risk of disease by distributing and increasing the areas to which the packs may resort for food.¹

In autumn, where a moor is near arable land, the birds will often come to feed on the stubbles and corn stooks; they sometimes come in hundreds, and from long distances. This is not, however, the universal rule, for in some districts Grouse feed very little upon the corn, and in some seasons they appear to frequent the arable land more than in others. It has often been observed that by improving the heather on a moor Grouse may be induced to feed less upon the stooks. The change is often accompanied by an improvement in the health of the stock, and this has given rise to the view that corn is an unwholesome diet for Grouse.²

In very severe weather the Grouse leave the high grounds entirely, and remove in packs many miles to the lower moors where they can find "black ground," or to a hill plantation where they can pick up a bare sustenance in the shape of various seeds. When they are very hard pressed, as ^{Seasonal} in the winter of 1894, they even flock to the turnip fields, and instances of their alighting on thorn hedges to pick the haws are recorded in the *Field* of that year. In Argyllshire they have been known to feed on birch twigs during the winter—settling on the trees to reach the woody buds.

The subject of the migration of Grouse is one which has engaged the attention of many naturalists; but there has been a tendency among observers to note only the abnormal cases, and from them to deduce a general rule. One great obstacle in the way of accurate observation is the difficulty of identifying the original point of departure of the wandering packs. In spite of the confident statements of gamekeepers that they can tell by the size and plumage of a bird that he has come from a certain district many miles away, it is more than probable that the newcomer has always had his habitation within a few miles of the neighbouring march, or even that he has never left his home, but has disguised himself by a sudden moult. In some districts undoubtedly the birds shift annually in vast packs from the high ground to the lower moors, and return again in the spring to breed.

On rare occasions migration takes place upon a much more serious scale,

¹ *Vide* chap. xvii. p. 392.

² *Vide* chap. viii. pp. 178-180.

when the whole Grouse population of a district, driven by hunger, rises in huge packs and works its way southward in search of food; this never happens unless a heavy undrifted snowfall has been followed by a hard frost, ^{Wholesale migration.} whereby a whole district is covered with an impenetrable sheet of frozen snow, thus cutting off all access to the heather. Such wholesale migrations often result in a complete loss of the stock, for the birds appear to lose their bearings, and though they may sometimes find a haven on some distant moor, where weather conditions are more propitious, several cases have been recorded of the packs being seen on the low ground 20 or 30 miles from the nearest hill, or even flying out to sea, whence presumably they never return.

In the case of normal annual migrations many opportunities have ^{Powers of flight of Grouse.} occurred for observing the power of flight of the Grouse. The following passage may be quoted from Macpherson in the *Fur and Feather Series*:¹

“When snow and sleet have driven them down from the hills they will then fly long distances. It is not at all unusual for Red Grouse to cross the Solway Firth at a point where the estuary measures two miles in breadth, and I have known them fly longer distances. They often cross the valley of the Tees, flying about a mile from one hillside to another.” And he quotes Millais, who says: “I have twice seen Grouse on the wing when they were crossing the ‘Bring,’ a wide channel which separates the islands of Hoy and Pomona, Orkneys. The fishermen told me this distance . . . was quite four miles across, and the birds must have come at least another mile on the Pomona side from the point where they left the moor.”² In Millais’ “*Game Birds*” it is stated that Grouse have been observed flying from Thurso to Hoy, a distance of over 11 miles.³ The following instances are vouched for by the Committee’s own correspondents. A gentleman in Banffshire, writing in January 1907, says: “Packs of Grouse are continually flying across the valley during stormy weather, some 5 or 6 miles between moors”; while in Cumnock, in Ayrshire, there are “two ranges of hills divided by a valley about 2 miles wide, with a moss lying in between. In the pairing season Grouse often fly at a considerable height over the valley between the hills.” Even during a Grouse drive a pack has been observed to leave the hill where it had been flushed, and not to rest until it had reached another moor 6 miles

¹ *Fur and Feather Series*, “The Grouse,” p. 36.

² Millais, “*Game Birds and Shooting Sketches*,” p. 53. London: Henry Sotheran & Co., 1892.

³ Millais, “*Natural History of British Game Birds*,” p. 54. London: Longmans, Green & Co., 1909.

distant. Longer flights are more difficult to authenticate; Harvie Brown states that "in the severe winter of 1878-1879, a pack of Grouse was seen crossing the Moray Firth in December, making for the Banff coast, as we were informed at the time by Sheriff Mackenzie of Tain. Much snow was lying at the time in East Sutherland and Caithness";¹ and Macpherson (*loc. cit.*) says also that "The Rev. M. A. Mathew records that a solitary Red Grouse was shot by Mr C. Edwards on the Mendips near Wrington, Somerset, in September 1885, and this he suggests must have crossed over the Bristol Channel, migrating from Breconshire."² Other records in "Birds of Essex," are quoted in Macpherson.³

We are indebted to the same writer for the following information upon the general habits of migration among Grouse.

"Their principal time for shifting about is in the evening after feeding, and again after 'becking' in the morning. But they are particularly restless on many moors about the end of September and in October, especially the female birds, and the first strong gale brings many of them off the hilltops, looking for more sheltered and genial situations.

"Birds of both sexes will fly a long distance to a patch of black heather during a prevalence of severe frost and heavy snow, but the hens shift about in packs more irregularly than their male companions, and they are less partial to the high grounds, but seek the lower portions of the moor, and such as are most screened from the east winds. Grouse netters say that in fine open weather the birds fly very long distances when shifting about the hills."⁴

Observations upon the wandering habits of individual Grouse have also been made where some peculiarity in the bird has made identification possible. An Ayrshire gamekeeper has told the Committee's field observer of a pure white Grouse which was seen and freely shot at on Glencairn and Upper Cree. It then disappeared, and was seen and shot at many times on a shooting 12 miles away. It was eventually killed by a gamekeeper 9 miles away from either of these moors, and now forms a stuffed specimen in a case in his cottage. All this happened in one season.

The question of the annual movements and migrations of Grouse are important as a guide to the best methods to be adopted for the regulation of

¹ Harvie Brown & Buckley's "Vertebrate Fauna of the Moray Basin" vol. ii. p. 152. Edinburgh: David Douglas, 1895.

² Fur and Feather Series, "The Grouse," p. 37.

³ *Ibid.*, p. 39.

⁴ *Ibid.*, p. 77.

stock. The fact that Grouse annually shift from place to place over a wide area forces one to the conclusion that co-operation is necessary rather than individual effort. For the same reason it is doubtful whether the benefit of introducing fresh blood (either in the form of eggs or of living birds) is confined to the moor on which the fresh blood is introduced. This remark would not, of course, apply to an isolated moor, or one in which for any reason the shifting habits of the birds are not fully developed.

Various opinions have been expressed as to the age which a Grouse can attain, and a few observations on the subject may be quoted. On a Yorkshire moor a cock Grouse, which was recognisable owing to its having a broken leg which stuck out permanently at right angles, was known to have lived for nine years in a wild state. An Ayrshire gamekeeper, one of the Committee's correspondents, can vouch for a Blackcock living twelve years, and is of opinion that Grouse live as long. Another correspondent, a Forfarshire gamekeeper, is sure that many of the old cocks on the tops are ten years old, and if appearance goes for anything the black old cocks so often killed on the high tops of many moors must have reached a not less patriarchal age. In view of the many dangers to which they are exposed the wild Grouse seldom gets the chance of dying of old age, and the duration of its life depends more on the severity of the shooting and the numbers of vermin than upon the bird's own longevity.

Observations on Grouse in captivity tend to support the view that they can live to a considerable age. Unfortunately, in every case reported to the Committee where a tame Grouse has reached the age of ten or twelve years the bird has died an accidental death.

CHAPTER III¹

THE CHANGES OF PLUMAGE IN THE RED GROUSE IN HEALTH AND IN DISEASE

By Edward A. Wilson

PART I.—PLUMAGE CHANGES OF THE COCK GROUSE

WHEN a large number of skins of the cock Grouse are arranged together, side by side, according to the month in which the birds were killed, it will be found that, even taking into account the differences of well-marked local variations in plumage, the series can readily be divided into two very distinct sets.

There is first a very marked uniformity in the plumage of the cock birds killed from the middle of November to the end of June; and likewise amongst those killed from the end of June to the middle of November. Seasonal changes of plumage.

These two periods, November to June and June to November, mark the two seasonal changes of plumage in the cock Grouse.

The first is a plumage worn throughout the winter, as well as during the courting and breeding season of the spring.

The second is a plumage worn throughout the late summer and early autumn.

It is necessary to lay stress upon this general broad division of the cock Grouse's plumage, and if a large number of skins can be arranged as suggested the time at which the Grouse has definitely changed from the one plumage to the other cannot possibly be overlooked. The birds obtained at the end of May are definitely in the darker and redder winter plumage, and those procured at the end of June are definitely in the paler and more buff-coloured summer plumage; those killed at the beginning of October are still partly in the paler summer plumage, and by the end of November all are in the darker winter plumage.

¹ Reprinted from the *Proceedings of the Zoological Society of London*, 1910.

It must, however, be added, that there is hardly a month in the whole year, or a Grouse skin in a collection of many hundreds covering every month of the year, in which one plumage only can be found unmixed with the other. This fact accounts largely for the misunderstanding which at one time existed, but which has now, we hope, been satisfactorily settled, in respect of the whole vexed question of moult and plumage changes in the Red Grouse, and their proper interpretation.

Without referring in detail to the points upon which differences of opinion have before now arisen, it may be shown that much misunderstanding upon this difficult subject is based upon a different rendering of facts into words, facts which were recognised and perfectly well explained by Mr Ogilvie-Grant in 1893.¹ Both he and Mr Millais have made the subject of plumage changes in the game-birds, and especially in the Grouse, a special study, and it must be admitted that there are very few points upon which they have touched which seem to require further explanation and still fewer points, if any, which can be brought to light for the first time in connection with the plumage changes of the Red Grouse. A monograph on the Red Grouse, such as the Report of the Grouse Disease Inquiry, would, however, be obviously incomplete without an account of the plumage changes of the bird itself; and it so happens that during the six years of the Grouse Disease Inquiry's existence the collection of some six hundred Red Grouse skins, representing every age, phase, and change of plumage in that bird, has given a unique opportunity for an independent revision of the work already done—an opportunity such as has never occurred before in the study of any single species of British bird for observing the effect of disease upon moult and feather growth. So it happens that although the work as it stands has been so nearly completed by the labours of the two ornithologists already mentioned, there are still points of interest to which attention may be drawn, especially in connection with the marked effect which parasitism and other wasting diseases have upon the moult and growth of feathers, and it is to this influence of disease that attention will be particularly drawn in the present paper.

It is important to note the extraordinary irregularities which so commonly occur in the plumage of the Red Grouse owing to disease, whereby the

¹ (1) "Annals and Magazine of Natural History" (6), xii., July 1893, pp. 62-65; (2) "Catalogue of the Birds in the British Museum," vol. xxii. November 1893, pp. 36-38; (3) "Annals of Scottish Natural History," July 1894, pp. 129-140, Pl. v. and vi.

deferred moult becomes in some years almost the rule, and the rule of health becomes almost the exception. It is a very difficult matter, ^{Effects of disease.} indeed, for any one who has not had the opportunity of examining an extensive series of Grouse skins, in disease as well as in health, and covering every month of the year, to come to any true conclusion about the moult. Diseased conditions often entirely mask the normal plumage changes from time to time, and it is far more important to realise this than to examine thousands of more or less healthy birds shot in the ordinary course of events in the shooting season. A study of abnormal plumage changes in diseased Grouse is essential if the discrepancies which arise in the moult of what are often wrongly considered normal birds, are ever to be explained. Once this point is grasped the question becomes much simpler, and it is because the Grouse Disease Committee has had such ample opportunity for studying both sides of the question that it has been deemed necessary to enter into these plumage changes at such length.

It is almost incredible that a moult should be deferred from one season to another, or even to a third, and that the right plumage should eventually be produced if the bird, by means of good food and good weather, is at last enabled to recover its health and grow any new feathers at all. ^{Effect on feet and legs.} It is interesting, and to some people, such as sportsmen and game-keepers, even useful to know that bare featherless legs and feet, which have so long been considered a sure sign of disease in the Red Grouse, may, in certain months of the year, be a natural accompaniment of really good health, while thickly feathered legs in the same month are a sure sign of deferred moult and of sickness. It is only when the proper season for the moult of the leg and foot-feathering is completely understood that we begin to understand the reason for attaching an unfavourable prognosis to heavy leg-feathering when the legs should have been featherless, and an equally favourable prognosis to bare legs when the legs should certainly have been bare (Pl. XIII., Figs. 1-2).

To return, however, to the two plumages of the healthy cock Grouse. They are distinguished by Mr Ogilvie-Grant as the *autumn plumage* and the *winter-summer plumage*, and he says further that the cock "has no distinct summer plumage."¹ It is perfectly easy to see what is meant by this, and also by the statement which follows, that the cock "retains the winter plumage throughout the breeding season."

¹ "Handbook to the Game Birds," p. 28. (Allen's Naturalists' Library). London: W. H. Allen & Co., Ltd., 1895.

Mr Millais also, in speaking of the cock Grouse, makes use of the expression *autumn plumage* which, he says, appears late in June; and he adds that the autumn plumage, together with the "*spring feathers*" (or what Mr Ogilvie-Grant considers the first beginning of the autumn plumage on the Grouse's neck), remain till the main moult in August and September.

Mr Millais also makes the following statement, which appears to be based on a misinterpretation. He says: "as a matter of fact the male Grouse sheds in September and August a plumage which is a mixture of its winter, spring, and eclipse feathers."¹

These so-called "spring" and "eclipse" feathers are no doubt, as Mr Ogilvie-Grant holds, the commencement of the plumage which is completed gradually during the summer months, and which he has described as the *autumn plumage*. It is naturally a little misleading to find the autumn plumage beginning to appear in early summer, but so long as the term is understood to mean the paler, more buff-coloured plumage with bolder bars of black, which begins to appear first on the neck of the cock at the end of May or early in June, and is eventually cast for the winter plumage in October, there need be no real misunderstanding.

That feathers of the previous winter plumage should be mentioned in speaking of the *moult* of this autumn plumage is also quite intelligible, since the old winter plumage of the breast and abdomen is being quickly shed and replaced by a similar new winter plumage at the time when the autumn plumage on the rest of the body is being cast. There are in addition very frequently a few feathers of the copper-red plumage on the chin really belonging to and remaining over from the previous winter plumage.

Instead of going into further details, however, with regard to the two moults and plumages of the cock Grouse, it will be simpler at this point to take its plumage changes in detail, successively month by month, explaining as nearly as possible what can be gathered from the examination of a series of skins such as has been brought together by the Committee, including as it does a great number of specimens in all stages of disease as well as in health.

These illustrate every month of the year and most of the local variations to be found in England, Scotland, and Ireland; and there are a sufficient number of sick as well as healthy birds to show the very great influence that disease has in altering the individual capacity for feather growth. Unless this effect, which results as a rule in the Red Grouse from excessive parasitism, is

¹ *In lit.*, "British Birds," for April 1910, vol. iii. p. 382. London: Witherley & Co.

fully recognised, there will always be misunderstandings upon the moult of this bird, for almost every Grouse in the country is to some extent infested with parasitic worms, and there are years when irregularity of moult is the rule rather than the exception. Moreover, it so happens that in autumn, when birds are being shot in large numbers, the survivors of the two worst months of the year for "Grouse Disease" mortality, that is, the survivors of May and June, are all convalescing; but they are convalescing with their plumage changes all retarded and put completely out of order and routine. In this way it is possible in September to kill two birds on the same day, both of which have the chestnut-coloured feathers of the winter plumage on the chin and throat; but upon examination it may be seen that in one bird the edges of these feathers are frayed and worn and the colour faded, showing that they have survived from the *previous* winter plumage; whereas in the other bird they are hardly free of the scaly sheaths in which they grew, and are really precocious feathers of the *coming* winter plumage. This is only one of the many traps which result from the deleterious influence which disease exerts upon a bird's capacity for feather growth and replacement, and so upon the regularity of its moult.

There is another point to which attention must be drawn before entering upon a systematic description of the monthly changes of feather in the cock Grouse. It is as to whether the autumn plumage of the cock can be correctly described as an "eclipse" plumage, comparable as it obviously is in character with the spring breeding plumage in the hen, but appearing just two months later and after the breeding season. In each sex the general change from winter to summer may be described as a change from a more richly pigmented, darker, black and chestnut, or rufous-chestnut plumage with rather fine transverse black markings, sometimes almost vermiculate in character, to a less richly pigmented, paler, buff or rufous-buff or tawny-buff plumage with characteristically broad black bars and transverse markings.

In each sex, moreover, the characteristic buff and black broad-banded summer plumage is given its special appearance on the dorsal aspect by the growth of feathers with large black centres and a few buff or tawny-buff subterminal bars of considerable width, and a terminal border or spot of the palest buff, which is a very conspicuous feature on the back of most hens, and often only less conspicuous in the cock. In the cock, however, this plumage appears just two months later, and is less beautifully developed than in the hen.

There is without doubt a general broad resemblance, firstly between the cock and the hen Grouse when the former is in its "winter plumage" and the latter in its "autumn plumage"; and, secondly, between the cock and the hen Grouse when the former is in its "autumn plumage" and the latter in its "spring plumage."

The perplexing fact is that these general resemblances are not synchronous in the two sexes, a peculiarity first observed by Mr Ogilvie-Grant, for, as already pointed out, there is an interval of two months between the moult of the cock and hen.

Cock and
hen moult
at different
seasons.

Again, it might reasonably be expected that, as the Ptarmigan and the Scandinavian Willow Grouse have not two plumages in the year, but three, some suggestion of the third plumage might be forthcoming in the Red Grouse. But the Red Grouse has only two moults. Mr Ogilvie-Grant, however, explains the position by saying that the buff and black plumage of the hen Grouse answers to the spring plumage of the hen Ptarmigan, while the buff and black plumage of the cock Grouse answers to the autumn plumage of the cock Ptarmigan. The grounds for this opinion will be considered later in the light of the possible effect which continued disease may have in permanently altering the season of the moult.

Beginning now with the cock Red Grouse in January, and taking its appearance from the ventral aspect first, the uniformity of the series is a very conspicuous feature. Every healthy bird is chestnut or rufous-chestnut and black, with fine, almost vermiculate black cross-lines over it.

Cock
Grouse in
January.

Even in the blackest birds the throat and fore-neck are always of a rich copper-red colour, with very little or no black edging at the borders of the feathers, which are usually barred with black only on the actual chin. Here there may be also more or less of white tippings, even to the formation of two white moustachios leading downwards from the gape, sometimes an inch in length. This may be a feature either of the black type or of the red¹ (Pl. II. and III.). In some very red and black Red Grouse the abdominal feathers are also freely and broadly tipped with white; and this may sometimes be seen even on the feathers of the upper parts (Pl. IV.) The legs and feet are thickly feathered, and are white, or white with brownish barring. The

¹ The whole chapter deals with the Red Grouse (*Lagopus scoticus* Lath.). The terms "black Red Grouse" and "buff-spotted or white-spotted Red Grouse" must not be confused with similar terms for other species of Grouse.

Pl. II.
(P.Z.S. 1910. *Pl. LXXIX.*)

*Univ. of
California*



Andre & Seigh, Ltd

MALE GROUSE, BLACK TYPE, IN FULL WINTER-PLUMAGE.

Pl. III.

(P.Z.S. 1910. *Pl. LXXX.*)



Andre & Seigh, Ltd.

MALE GROUSE, RED TYPE, IN FULL WINTER-PLUMAGE.

Pl. IV.

(P.Z.S. 1910. *Pl. LXXXI.*)



Andre & Sleigh, Ltd.

MALE GROUSE. WHITE-SPOTTED BIRD OF THE RED TYPE.

Pl. V.

(P.Z.S. 1910. *Pl. LXXXII.*)



Andre & Sleigh. L'd.

MALE GROUSE. RED TYPE, IN FULL WINTER-PLUMAGE WITH A
FEW BLACK-CENTERED FEATHERS OF THE PREVIOUS
AUTUMN-PLUMAGE.

claws are often in this month very long and strong. Occasionally a pale bleached feather of the preceding "autumn plumage" is to be found on the flanks, middle of the breast or neck, and may be recognised by its frayed edges; and occasionally (*e.g.*, No. 539), in a very backward bird, there may be many such worn and faded feathers on the chest and flanks, but such a case is invariably the result of sickness. On the dorsal side there is again, broadly speaking, a general uniformity of chestnut, bright or dark, or of blackish feathers, with fine black transverse markings; but in almost every bird there may be found a considerable number of the old black-centred "autumn plumage" feathers remaining, with their frayed and faded edges of whitish-buff (Pl. v.). On the lower back and rump the more worn and faded feathers predominate. The primary and secondary quills are all complete, and are but a few months old, having been renewed between June and August; and the same may be said of the rectrices.

The following points in the cock Grouse of January are characteristic.

- (1.) The rich copper-red, generally unbarred feathers of the throat and fore-neck (Pl. xvi., Figs. 3 and 4).
- (2.) The fine barring of the chestnut, dark rufous-chestnut, or blackish-brown of the back, with the scattered black-centred feathers of the last "autumn plumage."
- (3.) The thick, white feathering of the feet and legs, which soon becomes blackened and worn by the "burrens" or "colons," the charred stalks of old burned heather.
- (4.) The perfect flight-feathers of the wings and tail.
- (5.) The very large claws.

In *February* the cock Grouse is still in the darker winter plumage. Young, sheathed and growing broad-barred feathers, the remains of the "winter plumage," may still occasionally be found on the hind-^{February.} neck, nape, and head in backward birds.

In *March* the cock Grouse normally shows no change; but towards the end of the month in exceptional instances individual birds may be found with a few precocious feathers of the autumn plumage making their appearance on the back of the head and neck. These are very probably^{March.} feathers irregularly developed to take the place of those which have been lost during encounters with other males.

In *April* the cock Grouse still shows no change. In this month there are

often greatly increased opportunities for the addition of skins to a collection, because it happens to be a month of very high mortality from April. "disease." The birds are found and can be collected not only by the keepers who are out early in the month in search of fox-earths, and who are generally also burning heather about this time, but also later by the shepherds who are constantly ranging the moor in the lambing time. During the last five years there has been a great accession of Grouse skins to the Inquiry's collection in March with a very large proportion of males badly diseased, and comparatively few birds in perfect health. Therefore, in the series of skins of cock birds representing the month of April, the great majority are very backward. Healthy birds have still the old, rich, red, copper-coloured throat of the winter plumage, and fresh-looking "autumn" feathers round the neck, upper back, and mantle, while the winter and old autumn plumage of the rump and back is bleached and faded. The backward birds are easily picked out, as they have not yet assumed their "winter" plumage, and are still mostly clad in old, worn autumn plumage of the previous year. If an April bird has newly and thickly feathered legs and feet, it means, almost certainly, that the "winter" plumage has been put on very late. The healthy Grouse should now be moulting the feathers of the feet and legs, so that bareness or lack of feathers becomes in them a sign of health in *April*, and thickly feathered legs a sign of sickness; this is the precise contrary of what has almost become proverbial on the moor, that bare legs indicate disease; though for the later autumn months the saying is quite true.

In *May* the preponderance of cock birds found dead, and therefore of skins of cock birds in the May collection showing belated moult, is again a large one. The healthy cock is still in his much-worn winter May. plumage, but on the head and neck some feathers of the new autumn plumage are beginning to make their appearance (Pl. VI. and VII.).

In *June* as a rule, the mortality amongst adult birds, due to Strongylosis, is coming to an end; but for the young chicks June and July are often fatal months owing to Coccidiosis. Late in June the healthy June. cock Grouse can at last be said to have changed into his complete "autumn plumage." The winter plumage persists only on the abdomen and lower breast, on the actual chin which is blackish with a few white spots, and on the throat, where a few red feathers still remain. The moulting of the quills and tail feathers commences towards the end

Pl. VI.
(P.Z.S. 1910. *Pl. LXXXIII.*)

*Wm. of
Columbia*



Andre & Seigh, Ltd.

MALE GROUSE SHOWING MARKED BEGINNING OF THE
AUTUMN-PLUMAGE ON HEAD AND NECK.

Pl. VII.
(P.Z.S. 1910. *Pl. LXXXIV.*)



Andre & Sleigh, Ltd.

MALE GROUSE CHANGING FROM WINTER- TO AUTUMN-PLUMAGE.

of the month. The rump and back are now completely covered with new black-centred feathers carrying broad-barred buff and black bands, and a few have a whitish terminal spot, similar to that found in the female. The head and neck, breast and throat, are now clothed in broad-barred buff and black feathers, quite distinct from the more chestnut and more finely black-marked plumage of the winter. It is impossible on seeing a series of the birds showing this distinctive change to avoid noticing how closely this autumn plumage of the cock approximates to the nesting plumage of the hen, and yet it is wrong to think and to speak of this "autumn" plumage as an "eclipse" plumage, for it has arrived in the cock just two months later than it is normally due in the hen—far too late to be a breeding plumage. It appears almost as though the pathological postponement of the moult, a postponement which is, after all, nothing but a sign and a symptom of disease, has gradually developed into a normal habit in the life of the bird, and one is led to think that this habitual disability in the cock Grouse, which results from Strongylosis during the nesting, courting, and breeding season (a disability which causes the death of about eight cocks to every hen in April and in May), may have caused the alteration in the season of the moult, simply because the *vis vitæ* of the cock bird, insufficient as we now know it to be at the close of winter for the ordinary calls of reproduction, would be still more disastrously insufficient if preceded by an early moult.

At the present time the cock undoubtedly breeds in the winter plumage, without any further acquisition of new feathers, and, as has recently been pointed out by Mr Ogilvie-Grant, what have been regarded by Mr Millais as new "spring feathers" on the neck are in fact the *old* autumn feathers, which on that part of the body do not become worn and faded.

That any feather of the Grouse, either in the cock or in the hen, was ever altered as to its pigment either in pattern, or in tone, or in any other character, when once it had completed growth and had been cut off from the circulation, is at present an assumption which is not well supported by the physiology of feather growth.

Metchnikoff's observation upon the migration of leucocytes into hair and their action in removing pigment cannot for one moment be adduced as conclusive proof that the same thing may happen in the case of a full-grown feather. While the circulation is active in the feather shaft, and for as long

Possible
cause of
postpone-
ment.

Change in
pigment
improb-
able.

and in so far as it continues, pigmentation may be altered, but once the circulation has ceased beyond the entrance to the base of the shaft, and once that the feather, although still attached to the epidermis, is cut off from the circulation in the deeper living layer of the skin, then the feather is no more likely or able to change the pigment which is responsible for its pattern or its colour than would be the same feather had it been plucked out and kept entirely separate from the bird.

Once the feather is full grown, and the circulation in it stopped, there is no reason to believe that any thing can alter it save sunlight and water, and oil supplied as an external unguent from the oil gland. That appearances are most deceptive in this respect must be allowed. Feathers may be collected from the flanks of hen Grouse which show every possible graduation between the almost vermiculate flank feather indicating the perfect winter plumage, and the broad-barred breeding-season flank feather of the summer hen. But it is very much more probable that the growing period of these ambiguous or intermediate feathers is one of great susceptibility to outside conditions, as we know to be the case in respect of the metabolic processes which are taking place within the hen bird at the time. Pigment is indisputably a product of tissue metabolism. It is often probably a mere waste product, but it appears at times to serve a special function notwithstanding. It is also certain that pigment is a production whose appearance, or failure to appear, is open to considerable vicissitudes in consequence of small recognised changes in physiological condition, and of some less easily recognised changes in the general metabolism of the body.

In the hen Grouse during the breeding season we know that pigment production is very actively at work, for we know that a very large amount is being produced for excretion in the pigment glands of the lower part of the oviduct. This pigment, moreover, is precisely of the shade and colour which is characteristic, not of the breeding plumage, but of the winter dress of the hen and the cock Red Grouse. It is normally deposited in abundance on every egg, but on the other hand it may abnormally fail to be deposited or even produced at all, not only in the eggs in the oviduct, but in the circulating blood of the bird's whole system. Thus the feathers, instead of becoming buff or brown, reddish or even black as they proceed in growth, may be any intermediate paler shade of buff, or even white, a character which is due generally to the complete absence of all pigment granules. The place of

the pigment in such feathers is probably taken by shining air globules, as it is in the hair and feathers of the majority of white animals and birds.

It is thus easier to believe that a sudden check, either by a change of temperature, or by wet and cold, or by want of sunshine, or by change in food, has for the time so far affected the tissue metabolism of the bird that a feather which began to grow upon a circulation lacking pigment particles, and which was therefore originally planned for the paler plumage, may, by a sudden increase in the metabolism of the bird, and so in the output of waste products to the blood, be completed as a feather of the more deeply pigmented plumage, thus producing a feather with the characters of both.

This is a plausible explanation, but is still open to some doubt, for the difference between the broad-banded buff and black flankfeather of the nesting hen, and the dark red-brown finely cross-lined feather of the same bird in winter, is obviously greater as regards pigment distribution than as regards the actual quantity of pigment deposited in the feathers.

If there are, as has been held, distinct pigments, such, for example, as buff, black, and orange-red, in the various colour-tones of the Red Grouse, it becomes easier to see that the loss of the red pigment, which is utilised for the eggs, leaves the buff and the black in greater quantity for the nesting season plumage. In the winter all three would once more be available.

The fat of the nesting hen is distinctly rich in colour, but in no case that we have seen has it amounted to the orange-coloured fat which is often seen in overfed Pheasants, and quite commonly in Gulls and Terns which have been feeding on red crustaceans. In these birds the orange-red fat or oil, tints not merely the fat beneath the skin, but even the white feathers of the breast and body often present a very beautiful rosy flush.

The whole question of pigment production and pigment distribution, intimately connected as it is with the question of the excretion of waste products and the deposition of fat, both in health and in disease, has not reached a stage which admits of dogmatic statement upon the subject of pattern change in feathers without moult.

One recognised method of changing a colour-pattern in feathers without moult is to be seen in the male of the familiar House Sparrow, which produces a handsome jet-black cravat in the breeding season, where before was a nondescript greyish throat; and this it does by the simple process of

shedding the grey ends of the feathers, leaving the blacker parts exposed. This method is common among birds, but the Red Grouse has been credited with changing *in situ* the colour and pattern of the flank feathers. Now, with still less reason as it seems, the cock bird has been credited by Mr Millais with achieving his summer or breeding plumage "for the most part by repigmentation and pattern change of most of the winter feathers below the neck."¹

This view cannot be upheld physiologically, and there is much to support the contention that the feathers which are believed to effect this change of pattern without moult are actually new growing feathers. This can readily be shown by the demonstration of their unshed sheaths. The misleading birds are again in this case the cocks which have been too sick to shed the previous "autumn plumage," and so are still struggling, with increasing success as the food improves, to produce a "winter plumage," which they should, and would in health, have achieved in October.

That the cock bird should moult the feathers of the legs and feet between March 30th and June 17th is no longer difficult to understand when the prevalence of Strongylosis is fully grasped. No bird is safe from the nematode infestation, and we are led to think that the majority of cock birds are so badly infested that they are forced to defer the autumn moult which should precede that of the previous winter. It is therefore obvious that between March and June there will be every stage of good or bad leg and foot-feathering between the newly acquired thick, white winter stocking of the sick cock, and the naked featherless clean moulted leg and foot of the really healthy male bird in June. In July, again, the healthy cock bird will be found beginning to produce white feather tips over the legs and feet.

In *July* the general appearance of the healthy cock is much lighter in colour-tone, and much more broken and mottled in pattern-character than that of the same bird in the winter. The claws are in many cases now ready to be shed, and the primaries, secondaries, and tail feathers are in moult. Some six or eight new clean-grown primaries are often to be found in July, and the long tail coverts are broad-barred buff and black.

In *August* the cock Grouse has, of course, the appearance of full summer or autumn plumage, but it requires very little examination to see that he has already begun to put on feathers of the winter plumage.

¹ "Natural History of British Game Birds," p. 40.

He now rapidly sheds the old feathers of the last winter's plumage which remained throughout the summer upon his breast and abdomen, and replaces them with the exceedingly handsome narrow cross-barred red or brown or blackish feathers of the coming winter plumage. There is no second moult or replacement of these feathers of the breast and abdomen in the cock. Once in the year is enough for this special area, and the feathers that "carry through" are wholly of the winter plumage. They are often broadly tipped with white. The chin feathers which survived with those of the breast and abdomen are now also replaced by new ones. It is noticeable that in the Ptarmigan it is also the white feathering of the chin and of the breast and belly, as well as of the wings and tail, which is changed once only in the year, exactly as with the winter plumage of the Grouse. It suggests that these two plumages are analogous in each species.

The plumage changes in the Ptarmigan are, strange to say, quite different to the changes in the Grouse. The Ptarmigan has three distinct moults and plumages in the year. The Red Grouse has but two.

In August, as has been said, the cock Red Grouse has begun to put on his winter plumage. The feathers of the breast and abdomen are full of sheaths and sheath-scurf, the growth of these feathers being very rapid and often scarcely noticeable. On the rump, back, and to a less extent on the shoulders, new rich red-brown feathers finely marked with black lines are showing here and there. Primaries, secondaries, tail feathers, and coverts are now replaced by new and blackish feathers with perfect and unbroken outlines. Even a few new rich copper-coloured feathers are appearing as isolated touches of bright colour amongst the faded broad-barred autumn feathers of the upper breast. The feet and legs are bare, save where new white feather tips are just appearing through the skin, and the claws of all the healthy birds are being shed (Pl. XIII., Figs. 3, 4, 5, 6).

In *September* the chin and throat of the cock Grouse are a mixture of many pale autumn feathers much worn and faded, and a few new copper-red ones. Most of the frayed "autumn plumage" feathers are now falling out. The breast and abdomen, wings and tails, are clothed with altogether new feathers, while the head and neck, back, shoulders, rump, and coverts of the tail are in a transition state, the "autumn" feathers frayed and bleached at the tips, contrasting with the new rich chestnut and darker brownish winter feathers with their fine black transverse markings.

The feathers of the legs and feet of healthy birds are rapidly growing to form thick, white stockings for the winter. Bare legs in September are a sign of belated moult or, in other words, a sign of sickness.

In *October*, for the first time since the preceding winter, the red and black varieties of Red Grouse become once more conspicuously distinct. This result is due to the new growth of fully pigmented feathers, either red or black, upon the under surface of the body. The upper neck is rapidly becoming copper-red. The chin and throat still show a proportion of the faded buff "autumn" feathers among the red, the former looking spotty and pale. On the back the new chestnut and black feathers are rapidly replacing the faded autumn feathers. Some perfectly healthy cocks still look as if in "autumn plumage," while others, on the contrary, have nearly completed their winter dress. The legs and feet are thickly covered with white feathers, and the nails are uniformly small, as the old claws have all been shed. Their growth, however, is extremely rapid.

In *November* and *December* the cock Grouse drops most of the remaining "autumn plumage." By the end of the latter month his moult is complete, but on the neck and back a greater or lesser number of these autumn feathers are retained till the following summer.

The most striking characteristics of the winter plumage are the rich copper-coloured neck and throat, and, in the darker varieties which are common in the Scottish Highlands, the contrasting blackness of the upper breast and abdomen often broadly flecked with pure white tips.

Amongst the cocks there are several well-defined and easily recognised varieties, which seem to have a certain regularity of distribution geographically. These will be considered below.

It must not be forgotten that, owing to innumerable efforts, which have been more or less successfully made from time to time, to transfer Red Grouse from one part of the country to another, the distinction of local variations has become a thing of the past, and is now impossible except upon a very limited scale. The attempt, however, can be made, and the number of specimens in the Committee's collection of Red Grouse skins makes it possible to arrive at some conclusions.

PART II.—PLUMAGE CHANGES OF THE HEN GROUSE.

The two changes of plumage in the hen Grouse are completed, as has already been explained, in the one case by the end of April or the beginning of May, and in the other case by July and August.

The actual feather changes in both cock and hen are really very comparable in character, notwithstanding the difference as to season; and allowing for the difference of two months which makes the moult in the two sexes asynchronous, they may be described and explained in very much the same terms.

Seasonal
changes of
plumage.

Mr Ogilvie-Grant was the first to draw attention to the exceptional want of agreement in the seasons chosen by the two sexes of the Red Grouse for their moult, and as in the cock's plumage he makes use of the terms "autumn" and "winter-summer" or "winter" plumages, which have therefore been used here, so in speaking of the hen's plumages it will be well to adhere similarly to the expressions used by him, and to call them "summer" and "autumn-winter" or "autumn" plumages.

Explana-
tion of
terms.

Exception may be taken, and indeed has been taken, to these names, as being inappropriate and inexact, but they are sufficiently exact for all practical purposes, and so long as moults and plumage changes are not completed in a week, but are spread over a period of several months, so long will there be some inexactitude in the terminology of these moults and plumages if they are named according to the months or seasons. It is immaterial so long as the term is sufficiently defined, for it is obviously impossible to use a term so exact as to require no definition.

The hen Grouse moults twice in the year, and wears her "summer plumage" as the breeding dress from April to July, and her "autumn" or "autumn to winter" plumage from August to March. These changes may be expressed in terms of comparison with the cock, as a case of plumage change in which the hen has two annual moults, exactly as has the cock, but both moults occur two months earlier in the hen than in the cock.

The hen's "summer" or breeding plumage is a very beautiful dress,

variable to a considerable extent it is true, but yet having a general uniformity which becomes the more obvious as a greater series of skins in any particular phase of plumage is examined.

Opportunities for even seeing the hen Grouse, to say nothing of obtaining her skin, in the full breeding plumage are rare; and thus it happens

that, even in the large series of Grouse skins at South Kensington and at Cambridge, this phase is only poorly represented.

Difficulty of
obtaining
specimens
of nesting
plumage.

The Committee has been to some extent more fortunate, and has obtained a great many skins of hens in the summer plumage (see p. 54 and Appendix D), so that points of resemblance can be noted at sight, and individual variations perforce take their proper places. It has been a marked feature in the whole collection of six hundred skins that as the series grew, and the general uniformity became more marked, the individual variations of which we were inclined to make much at first, became gradually relegated to their subordinate position.

Uniformity, albeit with endless minor variations, is the rule in the Grouse as it is in every other creature that leads an unprotected existence under natural conditions. How long it will continue in the protected, often over-protected, Grouse remains to be seen. It is possible that such variation as already occurs is to some extent a modern development; but on this point there is at present insufficient evidence to amount to certainty.

Beginning once more with *January*, it may be said that in this month some hens, when examined on the under side, are hardly distinguishable by

their plumage from some cocks (Pl. VIII.). On the dorsum it is different, and a healthy hen in January is unmistakable owing to the terminal spots of buff which appear almost invariably, though occasionally in limited numbers, on the feathers of the back. In some healthy hens the chin is sometimes still pale buff in colour, owing to the persistence of summer-plumage feathers of the preceding year. The throat and fore-neck, on the other hand, are copper-red, but rarely so uniformly red as in the cock (Pl. XVI., Fig. 1). The copper-red feathers seem to begin on the fore-neck and proceed towards the chin, so that the chin often remains buff and black when the throat is already red. Except in very backward birds, which have been sick, the old and faded broad-barred feathers of the flanks are never found in January. The legs and feet are white and thickly feathered, and the claws are long and strong.

Pl. VIII.
(P.Z.S. 1910. *Pl. LXXXV.*)



Andre & Siegh, Ltd.

FEMALE GROUSE, BLACK TYPE, IN AUTUMN-PLUMAGE.

10. 11. 11.
11. 11. 11.

Pl. IX.
(P.Z.S. 1910. *Pl. LXXXVII.*)



Andre & Sleigh, Ltd.

FEMALE GROUSE, RED TYPE, CHANGING FROM WINTER- TO
SUMMER-PLUMAGE.

TO VINU
ANBOHIAO

Pl. X.

(P.Z.S. 1910. *Pl. LXXXVI.*)



Andre & Sleigh, Ltd.

FEMALE GROUSE IN FULL BREEDING-PLUMAGE.

In *February* the bird is still in the same plumage as in January. In a few forward birds the feathers of the summer dress are beginning to make their appearance on the back of the neck about the middle of the month. February.

In *March* the change from autumn plumage to spring breeding plumage is, in healthy birds, now quite unmistakable, though many birds are very backward owing to disease. All doubt as to the sex of healthy birds, whether from above or below, is now removed. The broad-barred buff and black feathers of the flanks are now appearing, and are most conspicuous and characteristic, while the whole of the lower breast and abdomen covered by the red-brown or red-black finely barred feather of September growth are still in excellent condition and remain unchanged (Pl. ix.). The feathers of the chin, throat, neck, and upper breast are now mixed with broad-barred black and yellow feathers in forward birds; while in backward birds the throat and fore-neck may still be clad in copper-red feathers. The legs and feet are already looking worn and less well feathered, but the claws are long. March.

In *April* and in *May*, for the simple reason that many hen Grouse died of "Grouse Disease" in these months during the six years of the Inquiry, the proportion of skins of backward hens is large. The birds thus picked up dead carry one immediately back again to winter, for April and May. although they ought by this time to be putting the finishing touches to their spring plumage, they are, in fact, but just succeeding in the belated effort to put on the autumn dress. They are thus a clear six months late, and afford the most misleading seasonal characters imaginable. Their legs and feet, instead of being worn and almost moulted clean, are at last, after a winter spent with almost naked legs, well-clothed with thick white feathers. The appearance of the legs therefore in the hens, as in the cocks, is totally misleading to the keeper or to the sportsman who considers bare unfeathered legs to be a sign of "Grouse Disease." This holds good for autumn only, and in spring precisely the opposite is the case, for in April, May, and June none but healthy birds have naked legs and feet. The general character of advanced and healthy birds towards the end of April and in May is that of a complete spring plumage. The whole of the upper parts are broadly barred with buff and black, and marked with conspicuous terminal whitish buff spots or bars (Pl. x.). The under parts, again, are

broadly barred with buff and black, from the chin to the throat and neck, over the breast and down the flanks, while the central lower breast and abdomen are still in the autumn plumage of the previous September (Pl. XI. and XII.). White terminal spots may, of course, be present on the breast and abdomen. These are a local or an individual character which will be mentioned later in dealing with varieties of feather pattern and coloration. The flank feathers of the hen in the full spring plumage show much diversity of pattern. This diversity even in the same individual bird has led to the belief that the pattern may be changed in an unmoulted feather from the autumn plumage arrangement of red-brown and reddish-black finely barred with lines of black to a much bolder barring of buff and black. It has been surmised, from the examination of single feathers, that the change commences in the centre of the feather on either side of the shaft, and gradually produces another pattern of a totally different colour. But can this be possible in a feather which has long been fully grown, and which has presumably been long cut off from any blood or lymph supply, and which is as dead as if it had been shed? (Pl. XII.). It is almost certain that re-arrangement of the pigment or of the pattern in this way is out of the question, and the reasons for this view have already been discussed.¹

The legs and feet of the hen Grouse in April and in May are very poorly feathered, and the claws are very long (Pl. XIII., Figs. 3, 5).

In *June* the legs and feet are almost bare, and the claws begin to drop off (Pl. XIII., Figs. 3, 4, 5). The precise date of this shedding of the claws is again really a part of the moult, and is, in consequence, equally dependent upon the health of the bird. Sick birds which have survived the spring mortality are always late in the shedding of their claws, and equally late in the changing of their feathers. The claws are shed, both in health and in disease, but once a year, and the casting is synchronous as a rule with the disappearance of the autumn dress. The figures (Pl. XIII.) by which this process is illustrated require but little explanation. The whole of the year's growth of horny black nail becomes loose on the soft and growing vascular matrix, and when quite ready to be cast can be easily pulled off like a little cap. The young nail beneath is at first soft, pink and vascular and very short, but soon hardens and deepens in colour, and in a month or two has grown to be a useful nail of horn. The transverse or circular groove which is

¹ *Vide* pp. 37-40.

Pl. XI.

(P.Z.S. 1910. Pl. LXXXVIII.)



Andre & Seigh, Ltd.

FEMALE GROUSE IN FULL SUMMER-PLUMAGE.

Pl. XII.

(P.Z.S. 1910. *Pl. XC.*)



Andre & Sleigh, Ltd

FEMALE GROUSE, RED TYPE ; FEATHERS FROM FLANKS.

Female grouse, red type, feathers from flanks. Natural size.
 Fig. *a* and *c* (from No. 1864), *g* and *h* (from No. 226), and *k* (from No. 632), are varieties of the spring flank-feathers.
 Fig. *b* (from No. 575) is a flank-feather from a very black hen.
 Fig. *d* (from No. 1864) is an example of what is termed fine-barred, dark-red winter-plumage, with narrow black bars or lines on rather dark rufous chestnut, the latter being slightly bleached towards the tip.
 Figs. *e* and *f* (from No. 1864) and *l* and *m* (from No. 664) illustrate intermediate stages of colouration, the feathers probably having broken through the skin when winter-conditions prevailed, and having completed their growth under summer-conditions.
 Figs. *i* and *n* (from No. 664) illustrate the reasoning upon which is based the view just mentioned ; of these two feathers there is no doubt that *n* was being grown much later than *i*, and therefore more in summer-conditions, producing summer breeding-plumage.



Andre & Sleigh, Ltd.

FEET OF RED GROUSE: (1) NEW WINTER-FEATHERS AND NAILS; (2) FULL WINTER-PLUMAGE;
(3) (4) (5) and (6) SHOWING STAGES IN MOULTING OF NAILS.

- XIII. Grouse, red type, feet showing winter-plumage.
Fig. 1. Right foot showing new winter-feathers and new nails (No. 1177).
" 2. Left foot showing full-feathered winter-plumage.
Feet of grouse, showing replacement of nails.
Fig. 3. Right foot (No. 1148) with old nails ready to be shed.
" 4. " " in median vertical section.
" 5. Left " (No. 1167). 5a, old nails; 5b, new nails; 5c, shed nails.
" 6. Right " (No. 1185) with new feathers and new nails.

Pl. XIV.

(P.Z.S. 1910. *Pl. LXXVIX.*)



Andre & Sleigh, Ltd.

FEMALE GROUSE SHOWING BARE PATCH OF SKIN AND DOUBLE
LINE OF BARRED FEATHERS ON ABDOMEN.

Pl. XV.

(P.Z.S. 1910. *Pl. XCI.*)



Andre & Sleigh, Ltd.

FEMALE GROUSE, RED TYPE ; WORN UPPER TAIL-COVERTS.

left at the point of detachment of the old nail is quite a useful indication of age in cases where there is a doubt as to a bird being over twelve months old or of the year. The presence of the groove showing that the claws have once at least been shed is conclusive proof that the bird is more than twelve months old.

In *June* there is another characteristic appearance in the hens, namely the bare patch of abdominal skin which results from the shedding of the abdominal feathers, grown in the previous September. The loss of these feathers leaves a naked patch of skin on the abdomen of a hen that has been sitting, and this patch remains naked for the next few months (Pl. Bare patch on abdomen. xiv.). The general character of a June hen in health is that of the completed summer-nesting plumage, broad-barred buff and black over all the upper and under parts, excepting the abdominal area, the lower breast, wings, and tail. But it looks already somewhat faded and worn; and it is quite probable that in acquiring so perfect a plumage for sitting unnoticed on a nest built amongst the heather, the economic absence of the redder pigment in the feathers is in part a result of the acknowledged fact that for longer and more trying use, and for wear and tear in feathers, darker pigments are required, whereas for the short-lived and less exacting requirements of the summer plumage in the hen Grouse from April to June the buff and black feathers, with very much poorer wearing qualities, are found to be sufficient. The accompanying figures of a few worn-out and moulting feathers taken from a hen in summer plumage, show how distinctly better the black pigmented parts of the feather stand wear and tear than the yellow parts (Pl. xv.). Certain pigments have a value, therefore, of a very practical nature apart altogether from the æsthetic point of view of attractiveness, or the rather hypothetical view of assimilation to surroundings for purposes of safety or to assist in obtaining food. He would be unwise, however, who denied that all three factors play a part in the very beautiful nesting plumage of the hen Grouse.

It very occasionally happens that the hen Grouse, instead of retaining the redder plumage of the previous autumn's growth on the abdomen until it drops off during incubation, grows an almost universal spring plumage of buff and black broad-barred feathers covering the lower breast and abdomen as well as the remainder of the body from head to tail. A skin showing this condition is preserved in the National Collection, and there is an almost equally perfect specimen in the Committee's Collection, No. 919. This patch sometimes absent.

The more usual procedure is that the abdominal patch of autumnal plumage is lost during incubation, and is then quickly replaced by a renewal of the autumnal feathers when the spring plumage is also being shed. There remains, however, in the majority of birds, a very quaint growth of belated spring plumage, consisting of buff and black-barred feathers in two lines down each side of the centre of the naked patch, as though, for some occult reason, the intention to grow "spring-plumage" feathers upon this area had never been altogether lost. This peculiar persistence of belated intention shows itself as a patch of yellow feathers made up of the two lines of feather growth in the midst of a much broader area of the autumn red pigmented feather which one would expect to find all over the abdomen (Pl. XIV.). It is conceivable that a small persistent remnant such as this, having no obvious connection with the surrounding plumage at the time, or with the habits of the bird, or with the seasons, may yet have something to do with the third or lost "eclipse" plumage which is still to be found in the grey plumage of the Ptarmigan, but is almost completely lost in the case of the Red Grouse.

In *July* the summer plumage of healthy hens is much worn out, frayed at the edges, and very definitely faded, and the feathers are already dropping out. On the chin, throat, and fore-neck, new red feathers of the autumn plumage, looking rich and dark, are already making their appearance. The back is as it was, but faded, and the flanks are still conspicuously broad-barred with buff and black; but the abdominal bare patch is now growing new autumn plumage feathers with great rapidity from the centre outwards. The primaries and secondaries have now commenced to moult. There may be in July, in the hen, as many as six or eight old primaries in each wing with frayed tips, still to be renewed.

Precocious young birds of the year can still at once be distinguished from hens in moult, because in the former the dark red-brown black-lined autumn plumage is on the flanks, while the broad-barred buff and black, and rather worn-out chicken feathers are in the centre of the abdomen. In the adult the distribution is reversed. The broad-barred buff and black feathers of the spring plumage are on the flanks, and the redder fine-barred autumn plumage is appearing in the centre (compare Pl. XII., Figs. *a*, *c*, *g*, *h*, *k*, and *n*, with Fig. *d*). In skin No. 284 there seems to be an unusual compromise in a very backward hen, owing to disease. The compromise is between the

Peculiar
growth on
abdomen.

Distinction
between
young and
old birds.



1

2



3



4



5

HEADS OF : (1) (2) FEMALE GROUSE ; (3) (4) MALE GROUSE ; (5) PTARMIGAN, SHOWING SUPRA-ORBITAL COMBS.

XVI. Heads of Grouse.
Fig. 1. Female. No. 61, 22.i.06. Showing the black markings on the throat.
" 2. Male. No. 545, 17.i.06. Showing the uniform chestnut throat.
" 3. Female Grouse (No. 1269, 8.ii.08).
" 4. Male " (No. 1268, 8.ii.08).
" 5. Male Ptarmigan.

Pl. XVII.
(P.Z.S. 1910. *Pl. XCVI.*)



Andre & Sleigh, Ltd.

HEAD OF BLACKCOCK. SHOWING SUPRA-ORBITAL COMB.

broad-barred and the winter plumage with its very fine black cross-lines (Pl. XII., Figs. *e*, *f*, *l*, and *m*).

The legs and feet in July are naked, and the claws are very small; but the feathers are already showing through as small white points, not to be confused with broken shafts, which occasionally result from wear and tear in woody heather.

The plumage of the hen Grouse in *August* is well known. It has already been pointed out how, owing to the sudden increase of observation, and owing to the sudden arrival of opportunities for examining an enormous number of birds over the whole country during this month, there August. has sprung up an idea that disease amongst Grouse has a recrudescence in the autumn. But this is not the case. There are probably fewer diseased birds on the moor in August than there are in July. In July, No autumn outbreak of disease. however, they are never shot, and therefore not investigated, but in August they are carefully picked out of every bag, and, owing to the general interest in the question of disease, are almost always noticed, and in a large proportion of cases publicly notified. Hence the idea that disease makes a new start in August and September. As a matter of fact, however, these wasted birds are almost certainly convalescent. They have been diseased, and they are still suffering from disease, but thanks, in the majority of cases to their sex (for the bulk of the sickly autumn birds are hens), they have avoided actual death in the two highest mortality months, April and May. Once tided over these fatal months, the food and general conditions of life improve, the weight of the cock goes up, and the balance is again in favour of recovery for him; and although with the hen the exigencies of incubation and the cares of the family continue to handicap her until June and even July, she then rapidly begins to put on weight, and in August and September is once more on the way towards complete recovery. Many sick-looking "piners" are shot upon the moors in August, but it should be remembered that in that month they are recovering from disease, and not growing worse; while in September many that were not up to the average weight the month before will be practically normal and probably indistinguishable from healthy birds, were it not that their serious indisposition of the preceding months has put them behind their fellows in the matter of feather change.

In August, therefore, the Committee's collection of skins contains a large number of examples of hen birds showing deferred moult and belated growth

of feather. The normal healthy hen Grouse in August has already put off most of the broad-barred spring plumage feathers of her nesting dress, and is very much like the cock bird in appearance, with the same dark, red-brown vermiculate or fine-barred plumage underneath, white-flecked or not as the case may be, and with a mixture of old and new feathers above. The legs and feet of a forward hen are already showing quite a fair growth of white feathers, and the nails have all been shed. The claws are therefore short and rather soft, and the transverse sulcus or groove at the point of detachment is clearly marked. In the wings there may still be a number of primaries to be changed.

In the convalescent "piner," on the other hand, the case is often very different. She has still a most deplorably bleached and weathered breeding plumage on her, with worn-out feathers, frayed or ragged, often with saw-toothed edges, showing the unequal effect of wear and tear on the pale buff pigmented and black pigmented parts. The bird in this belated plumage has quite naked legs and feet and long unshed nails, or may at the most be just showing the points of a new growth of feathers through the skin; and in this state she is conspicuously shabby and ill to look upon in comparison with the splendid plumage recently acquired by her healthy sisters, and by the now almost universally healthy cocks. But the point above all others to be remembered in this connection is that this hen is convalescent, and still has a couple of months of good food and good weather, as a rule, in which to complete her convalescence before the winter comes.

If the spring outbreak of disease has been severe—that is, if the general conditions of the preceding winter and early spring months have been such as to conduce to a heavy and widespread infection of the Grouse with the larval *Trichostrongylus*—then both cocks and hens will be equally infested. But the breeding season and the concomitant needs of the two sexes are, from April onwards, quite distinct from one another.

The result of this is that there is often a large mortality of cocks in April and in May, and a much less marked mortality of hens, probably in the proportion of seven or eight cocks to one hen, but definitely occurring in the same two months.

There is no great mortality from Strongylosis in any other months of the year and after May, the cocks are suddenly relieved and rapidly recover,

Different
effect of
disease
in cocks
and hens.

so that by August there are almost no sick cocks; the hens, on the other hand, have still two very trying months to face, and although, thanks to the abundance of food, probably most of them succeed in struggling through, yet by August they have only just been freed of their more pressing cares and disabilities, and so a very great number are still found to be in very poor condition. The moment the disabilities are removed, however, they begin to recover, and it is this point which has so constantly been overlooked. Sick birds in August are convalescent, and however many there may be, it is not a sign of a new outbreak of disease, but a sign that the past spring infection was a heavy one, though less fatal than it might have been.

At the end of their own specially critical periods, the cocks have at any rate June, July, August, and September in which to pull themselves together by means of good food assisted by good weather; whereas the hens, at the end of *their* own specially critical period, have August and September. Hence the preponderance of sick-looking hens when the shooting begins, and the widespread, but erroneous, belief in a recrudescence of disease in autumn.

To return to the further consideration of the hen's change of plumage in *September*, her finest feature is now undoubtedly the clean new growth of bright red, or dark red or even black and white-flecked feathers of the breast and abdomen, with their narrow but even blacker markings. ^{September.} The whole of the feathers of this tract have now been shed, but they grow again so quickly that no bare skin is visible save in the middle area of the abdomen quite low down, where, as has been already pointed out, the new growth is of belated feathers coloured as in the spring plumage, and therefore quite different from those around them. There is still, as a rule, no accession of new red feathers on the chin or throat of the healthy September hen, or at the most but a feather or two. But in the sick hen there is still often a sprinkling of the old red feathers of the preceding autumn plumage, very faded, amongst the faded buff and black feathers of the belated spring plumage. On the back of even forward hens there is still a mixture of old and new plumage, and the scapulars are often faded to something like black and white, and are badly frayed at the ends. The wings have now almost completed their moult, but there may still be a primary or two to change, even in very forward birds. The legs and feet are rapidly becoming feathered for the winter, though in backward birds which have been sick they are

still quite bare, and now, of course, this feature may truly be taken to be a sign of sickness and disease, though in a convalescing bird.

In *October* one may find a very backward bird with as many as three worn-out primaries in either wing to change; but, as a rule, the wing is perfect, the primaries and secondaries and their coverts all completely new, and in the tail the rectrices are full grown. The legs and feet are now also fully feathered, though the thickness of the growth increases as the winter cold comes on. On the back the bird now looks fresh and richly coloured, from head to tail, but a close search will always disclose a number of spring-plumage feathers which have still to be thrown off. Underneath, the rich red-copper colour is gradually replacing all the previous buff on the chin and throat. The change "hangs fire" a little on the neck and upper breast, but it is still progressing, whereas on the lower breast and belly the rich red or darker winter plumage with its beautiful fine black cross-lines and pure white flecks is a very striking feature.

There are, in the Committee's collection of skins, a number of examples showing the result of disease in deferring the moult; many of these birds, even in October and November, have made no effort to get rid of the old, faded and completely worn-out spring plumage. The majority of these birds have been so diseased in spring that they have not bred at all. The ovaries have throughout the season shown no development, and there are no signs, even in the earlier months, of the shedding or development of ova or of any increase in size of the oviduct. They have been true barren hens. In some cases (*e.g.*, in No. 1247) there appear, in November, feathers of three separate plumages. There are the faded spring-plumage feathers of the current year, but mixed up with them here and there are new feathers of the autumn plumage coming, and here and there exceedingly old worn feathers of the autumn plumage of the year before. No. 1225, an October hen, shows exceedingly well how the bare, broody patch of the abdomen grows delayed broad-barred buff and black feathers instead of the fine-barred darker autumn-plumage feathers which surround the patch. These broad-barred feathers appear in two parallel rows, breaking through the skin of the broody patch on either side of the medial line; this growth is also well shown in a specimen at the British Museum of Natural History (Pl. xiv.).

In *November* the chief alteration is the completion of the autumn moult.

and the assumption of the autumn plumage. The feathers of the upper parts have black middles, and are barred with rufous - chestnut and ornamented with the characteristic white or buff-coloured terminal spots. November.

In *December* the hen is in full autumn-winter plumage. On the legs and feet she is well and thickly feathered; and on the under side the chin and throat are dark red, as well as the fore-neck, marked with broader black bars than upon the lower breast and abdomen, December. where the marking is of the finer type, and the colour distinctly of the redder and darker autumn plumage.

PART III.—LOCAL VARIATION IN THE PLUMAGE OF THE GROUSE.

The following notes are the outcome of an attempt to find some broad differences between Grouse from the Highlands, the Lowlands, the east coast and the west coast of Scotland, and from English, Welsh, and Irish moors.

It seemed possible that, with a large series of skins of a species peculiar to the British Isles and at the same time so variable, one might discover points in the coloration of the plumage or in the size of the birds which could be attributed to the varying physical conditions under which they live.

The artificial transportation of Grouse from one county to another, generally from the southern moors to the northern, often far removed from one another, with different food and climate, has no doubt to some extent confused the issue. But this is a difficulty which will increase rather than decrease, and it is possible that the purity of the British breed (at present the only species of bird peculiar to our islands), may before long be entirely lost by the introduction of a foreign species, the Willow Grouse, on the mistaken supposition that the latter is freer from the parasite of "Grouse Disease." The foreign species has already been introduced here and there, and there has been some interbreeding with our own Red Grouse. Hence there was some reason for thinking that, unless the opportunity for collecting a series of pure bred British Red Grouse skins had been taken by the Committee, the same wide opportunity might not have occurred again before the introduction of foreign species had become popular.

The Committee's collection contains five hundred and eighty skins of the Red

Grouse, including five hundred and forty adult birds of both sexes and forty chicks and pullets. These, however, cannot be taken all together in one series. It is essential, for purposes of comparison, that the male birds in their two plumages should be taken separately in two lots, and the females in a similar manner. Therefore the skins have to be divided as follows:—

	No. of skins.
Male birds in winter plumage	241
Male birds in autumn plumage	120
Female birds in autumn plumage	108
Female birds in summer plumage	71
Immature birds of the first six months	40

The largest series of skins is therefore that of the male birds in winter plumage, and it so happens that this set, both as regards sex and plumage, is best adapted by its general uniformity to give some result when arranged map-wise over a large outline of Scotland and England.

An analysis of the greater part of the collection of skins is given in the Table on p. 55.

Having thus arranged the skins into lots which are sufficiently uniform to allow of comparison, and having arranged one of these lots, the cocks in their winter plumage, for instance, according to the localities from which they were obtained, it becomes possible to make the following deductions:—

- (1.) That the general uniformity is very much more marked than might have been expected considering the character for variability which has always been attributed to the bird; the variability is lost in the mass, though it is visible in individuals.
- (2.) That, allowing for a good many exceptions, there is certainly a greater tendency to blackness in the birds of the northern Highlands than in those of the south. Or, one may say that in passing from the north of Scotland southward and westward, there is an increasing tendency to the bright red and dark red types of Grouse, which culminate in the very characteristically bright red bird of Wales and of the Midlands of England, in which the predominating colour of the feathers of the breast and under parts generally is red with

fine broken black cross-lines, while these cross-lines are sometimes almost absent.

- (3.) This gradual change from north to south of black, or red and black to dark red cocks, and farther south to bright red cocks is accompanied (speaking very broadly, for there are many exceptions) by a loss of the white terminal borders which characterise the feathers of the abdomen.

	♂		♀		Totals.
	Jan. to May.	June to Dec.	Nov. to April.	May to Oct.	
Caithness	22	3	5	3	33
Sutherland	12	4	2	8	26
Ross	6	16	3	4	29
Inverness	30	14	5	8	57
Nairn	0	1	0	0	1
Moray	11	0	1	0	12
Banff	5	0	0	0	5
Aberdeen	3	3	0	3	9
Kincairdine	2	0	2	0	4
Forfar	1	1	0	3	5
Perth	17	16	5	13	51
Argyll and Mull	19+1	5	0	9	34
Dumbarton	14	4	3	1	22
Stirling	1	3	0	4	8
Fife	1	0	0	0	1
Haddington	3	0	1	1	5
Midlothian	5	0	0	2	7
Lanark	1	1	0	1	3
Ayr	1	2	2	5	10
Arran	4	4	1	1	10
Peebles	2	1	0	0	3
Selkirk	7	4	0	4	15
Roxburgh	0	4	1	2	7
Dumfries	8	4	4	2	18
Kirkcudbright	5	3	1	0	9
Wigtown	0	1	0	3	4
Northumberland	9	1	4	2	16
Cumberland	1	0	0	4	5
Durham	0	0	1	0	1
Westmorland	8	1	2	1	12
Lancashire	2	1	1	0	4
Yorks	28	13	14	13	68
Derbyshire	1	0	0	1	2
Wales	10	0	3	0	13
Ireland	0	0	0	1	1
	240	110	61	99	510

There is no doubt that the blacker birds of the Highlands of the north of Scotland are more frequently white spotted beneath than the birds obtained

farther south. Nevertheless, the white spotting is not confined to the blacker or to the darker birds, for it may be quite a conspicuous feature in the bright red birds of Wales and England, though in the lowlands and in the north of England, especially in Yorkshire, it is a rare character, only exceptionally met with.

Mr Ogilvie-Grant, in his "Handbook to the Game Birds," 1896, says: "The ordinary varieties of the *male* may be divided into three distinct types of plumage: a *red form*, a *black form*, and a *white-spotted form*."¹

The *red form*, he says, "is mostly to be found on the low grounds of Ireland, the west coast of Scotland, and the Outer Hebrides";² and this statement is borne out not only by the Committee's collection of Red type, cocks. Grouse skins, but by the interesting collection made by Mr T. E. Buckley now in the Cambridge Museum. Similar birds have been obtained in some numbers from Caithness, Sutherland, the Lewes, and Inverness-shire. From Stirling, Selkirk, Northumberland, and Wicklow only one or two have been examined, but in Wales the red type is almost always met with. Welsh birds are often most typically and uniformly very bright red. Dumfriesshire also undoubtedly produces a large proportion of the same red type.

Bright red birds are not commonly characteristic of Ross-shire, Stirling-shire, or Northumberland, notwithstanding the fact that an occasional example of this type may be found in these counties. Dumbartonshire, however, and Argyllshire are said to produce more birds of a bright red type than other counties, and both these counties fall in with Sutherlandshire as forming part of the west coast of Scotland.

The following specimens have been figured to illustrate the red type of the cock Grouse:—

Pl. v. Upper surface: red type in winter plumage.

Male Grouse, No. 630. Wales, 18.3.07.

Pl. III. Under surface: red type in winter plumage.

Male Grouse, No. 407. Glendoe, Inverness-shire, 7.12.06.

Pl. VII. Under surface: red type, changing from winter to autumn plumage.

Male Grouse, No. 915. Forfarshire, 4.6.07.

¹ "Handbook to the Game Birds," p. 27. ² *Ibid.*, p. 28.

Pl. xviii. Under surface: variety of red type in autumn plumage.

Male Grouse. Loch Sween, 19.8.92. C. C. S. Parsons.

British Museum (Natural History), 92.7.13.1.

The second or *black form* of cock Grouse is, according to Mr Ogilvie-Grant, rarely met with, most of the black birds being mixed with the red or white-spotted forms. In the Committee's collection there are a few very good examples of the really black type, and they come from the following areas:—Caithness, Sutherland, Perthshire, Dumbartonshire, and Yorkshire. More or less typical examples have also been obtained from Ross-shire, Aberdeenshire, Morayshire, Kincardine, Stirling, Fife, and Lancashire. At Newcastleton the low-lying grassy moors are credited with the production of the black type of Grouse, while the other types are found on the higher heather ground.

The following specimen has been figured to illustrate the black type of Grouse cock:—

Pl. ii. Under surface: black type in winter plumage.

Male Grouse, No. 723. Perthshire, 4.4.07.

“The third or *white-spotted form* has the feathers of the breast and belly, and sometimes those of the head and upper parts, tipped with white. The most typical examples of this variety are found, as a rule, on the high grounds of the north of Scotland.”¹

White-spotted type, cocks.

This statement is again confirmed by the Committee's collection, although an occasional white-spotted bird makes its appearance farther to the south. It is, however, the exception in the south, whether it be on the red or black or intermediate type. The most marked examples of this white-spotted form have come from Caithness, Sutherland, and Inverness, while Dumfries, Perthshire, and Yorkshire have each provided one or two very fair examples. In Easter Ross birds are said to be most commonly dark red or black with white beneath. At Scrafton, Middleham, the majority have white beneath, and all are dark red or bright red. The predominance of white beneath is quite conspicuous in a geographical arrangement of a large number of skins, as a character of the north of Scotland, especially throughout the Highlands.

The following specimen has been figured, illustrating the white-spotted type of cock Grouse:—

¹ “Handbook to the Game Birds,” p. 28.

Pl. iv. Under surface: white-spotted form.

Male Grouse, No. 1377. Morayshire, 24.4.08.

Turning next to the female Red Grouse, no less than five distinct types are described by Mr Ogilvie-Grant: *a red form, a black form, a white-spotted form, a buff-spotted form and a buff-barred form.*

The difficulty in sorting hen Grouse into these classes is that a single bird may fall under three headings at once. A hen Grouse may be at once buff-spotted, white-spotted, and red or black, for the white spotting is an independent character and may occur on any type in the autumn plumage of the breast and abdomen, and this may also be definitely of the red or the black type.

In the Committee's collection, the first or *red form* is well represented from all parts of the country, and follows very much the same distribution as the red type of the cock Grouse.

Red examples were procured from the following areas:—Sutherland (3), Argyll (9), Arran (1), Dumbarton (1), Cumberland (1), Westmorland (1), and Wales (3), all bright red birds; Ross-shire, all dark red; Inverness-hens. shire (3), very bright red and (3) very dark red birds; Aberdeen (3), very dark red birds; Stirling (4), red birds, with very fine black markings on the breast. Perthshire, Moray, Kincardine, Dumfriesshire, Kirkcudbright, Northumberland, Durham, and Yorkshire were all represented by red hens, generally of the dark red type.

The following specimen has been figured, illustrating the red type of hen Grouse:—

Pl. ix. Under surface: red type changing from autumn to summer plumage.

Female Grouse, No. 226. Roxburghshire, 22.5.06.

The second or *black form* of hen is certainly, as Mr Ogilvie-Grant says, extremely uncommon, and only one or perhaps two of the Committee's birds should be included under this heading. Two others are, however, so dark as to come with difficulty under the category of red birds.

Caithness produced a really black hen bird (No. 418), the sex of which could not possibly have been determined from its plumage. It appears to be an old hen, which has assumed male plumage. Specimen No. 338 from Inverness is almost as dark a bird, and No. 559 is a very dark reddish-black bird. No. 414 from Dumbartonshire is similarly a case in which there seems to be more black than dark red.

The following specimen has been figured to illustrate the black type of female Grouse:—

Pl. VIII. Under surface: black type in autumn plumage.

Female Grouse, No. 418. Caithness, 31.12.06.

The third or *white-spotted form* is less rare, and, according to Mr Ogilvie-Grant, occurs as often as in the male. In the Committee's collection it is well represented by birds from Sutherland (No. 1336); Ross-shire, a bird of the red type (No. 176); and Inverness (No. 329). White-spotted type, hens.

It was less to be expected that examples both of the red type and of a darker type, bordering on the black, should have been met with in Yorkshire, Lancashire, and Westmorland. Single examples were also procured in Dumfries and Kincardine. There is a fine Irish example from co. Mayo in the British Museum (Natural History), No. 99 12.1.1.

The fourth or *buff-spotted form* of hen Grouse, said to be "much the commonest and most usually met with, has the feathers of the upper parts spotted at the tip with whitish buff."¹ This type is generally distributed, and the Committee's collection includes examples from Caithness, Sutherland, Ross, Perthshire, Ayrshire, Kincardine, Dumfries, Northumberland, Yorkshire, Westmorland, and Lancashire. Buff-spotted type, hens.

The fifth or *buff-barred form*, according to Mr Ogilvie-Grant, "is met with in the south of Ireland, and resembles in winter (autumn plumage) the ordinary female in breeding plumage, having the upper parts coarsely barred with buff and black. Very little is known of this last variety, owing to the difficulty of obtaining birds except during the shooting season."² Buff-barred type, hens.

The repeated endeavours of the Committee to obtain specimens resulted in one hen only being obtained from Donegal. This bird (No. 1217) was a very typical example of the buff-barred type, and it certainly differed from anything procured either in Scotland, England, or Wales.

Pl. XIX. Under surface: buff-barred form in autumn plumage.

Female Grouse, No. 1217. Donegal, Ireland, 17.10.07.

The nearest approach to it was to be found in four hens from Selkirkshire, and in hens from Inverness-shire, which were more accurately described as buff-barred than as buff-spotted. Single examples from Lanark, Midlothian, Roxburgh, Haddington, and Northumberland might be classed in the

¹ "Handbook to the Game Birds," p. 28.

² *Ibid.*

buff-barred type, and the females from Yorkshire were all rather of the buff-barred type, but none of these birds had quite the same markings as the Irish example. See Pl. x., female Grouse, in full summer plumage, Scottish buff-barred type.

Pl. xviii., xx., xxi., and xxii. represent abnormal varieties of the Red Grouse, and are drawn from specimens in the British Museum (Natural History). They are described in the explanation of the plates.

Two points in connection with the practical distinction of old Grouse from young, and of cock Grouse from hens, are of perennial interest both to the gamekeeper and to the sportsman. No discussion is more apt to produce different opinions than that which arises upon the age or the sex of Grouse in certain stages of moulting, either at the luncheon - hour upon the moor or in the game - larder when the day's bag has been overhauled, and hung upon the hooks. It must be admitted that there are individual cases occurring not rarely, in which it is almost impossible to tell the sex until the bird has been cut open and the internal anatomy examined. In these doubtful cases the only way to settle the point is to cut the bird open down the middle of the abdomen, carefully turn over the whole of the intestines from the right to the left—that is, from the bird's left side to the bird's right side—without tearing the attachments, and then, having exposed to view the flattened reddish kidneys which lie closely packed into the inequalities of the backbone and pelvis, to see whether an ovary or a testis is revealed overlying the uppermost portion of them.

In the breeding season, and in a breeding bird, there can be no doubt whatever as to the sex, for the ovary is a conspicuous bunch of more or less developed ova in the hen; and in the cock the testis is a conspicuous round, white object as large as the kernel of a good-sized hazel-nut on each side of the backbone.

There is but one ovary, and it lies always on the left side of the backbone of the bird. There are two testes, one lying on each side of the backbone, the left one generally at a slightly lower level than the right. This development of the ovary only on one, the left side, is the reason for advising the examination to be made as described above, on the left side always. One testis or the ovary cannot then be missed.

If the bird examined thus is not breeding, as may often be the case

Method of
ascertain-
ing sex.

Ovaries
and testes.

Pl. XVIII,
(P.Z.S. 1910. *Pl. XCVII.*)



Andre & Siegh, Ltd.

MALE GROUSE SHOWING ABNORMAL ERYTHRISM.

Pl. XIX.
(P.Z.S. 1910. *Pl. XCIVII.*)



Andre & Sleigh, Ltd.

FEMALE GROUSE, BUFF-BARRED TYPE.

Pl. XX.

(P.Z.S. 1910. *Pl. XCIX.*)

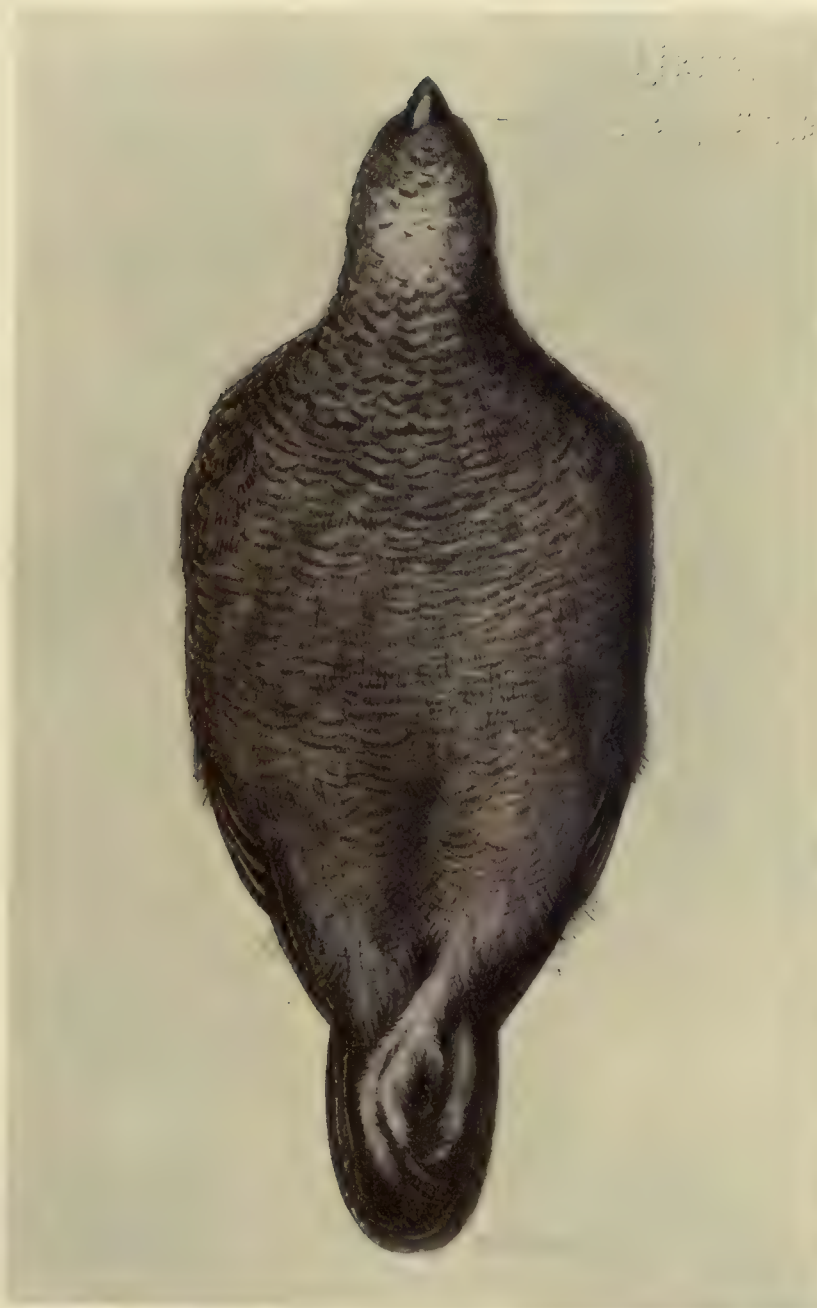
W. H. OF
CALIFORNIA



Andre & Sleigh, Ltd.

FEMALE GROUSE, ABNORMAL YELLOW VARIETY.

Pl. XXI.
(P.Z.S. 1910. *Pl. C.*)



Andre & Seigh, Ltd

FEMALE GROUSE, GREY VARIETY.

Pl. XXII.
(P.Z.S. 1910. Pl. CI.)



Andre & Seign, Ltd.

FEMALE GROUSE, GREY VARIETY.
(Type of *L. persicus*, G. R. GRAY.)

with birds found dead of disease in April and in May, the discovery of the ovary is still a matter of comparative ease, and the discovery of the testes even easier. The testes are always somewhat enlarged in the spring months, whether the bird be diseased or not, and they may be the size of a pea or larger, and will generally be white. The ovary may be small, but will always be like a portion of hard cod's roe, in which the ova, though no bigger than a pin's head, are distinct and numerous. The undeveloped ovary of an adult female Grouse would about cover a threepenny piece, but is long and triangular in shape rather than circular.

The oviduct in a breeding hen is a large and conspicuous duct, and may, of course, contain an egg with the shell in course of formation, being pigmented in preparation for laying. The oviduct in a barren bird, or in a hen at other times than the breeding season, is a very much less conspicuous object, and is less easily found than the small and undeveloped ovary.

If no ovary is seen, but a very small blackish, or whitish, or parti-coloured object is found in its place which is suspected of being a testis, the intestines must then be gently separated from their attachments about the middle line of the back, and the other testis must be sought for in about the same position on the opposite side. Even in a young bird the ovary shows ova with sufficient distinctness to make doubt as to its sex an impossibility; but in a very young male bird the testes may be so small, and, being very often black, may look so unlike what is expected that both should be sought for and found before arriving at a certain conclusion as to sex.

It is easy, if the intestines are roughly handled, and the attachments torn carelessly away, to carry away the testes or the ovary from their proper position, and to remove them with the intestinal attachments. The peritoneal folds are delicate and require careful handling, and they overlie the generative organs and the kidneys; but a very little practice will enable any one to do the necessary dissection with certainty, and to arrive at an irrefutable diagnosis as to sex.

It may be said that there is no other infallible means of arriving at the sex of a Grouse at certain times of the year, for it has so often happened that experienced and careful gamekeepers, who have handled Grouse for a lifetime, have certified a specimen as a cock, when the specimen has turned out to be a hen, and *vice versa*. The mistake is unavoidable and excusable,

for in certain individual Grouse in the autumn-winter plumage there is no reliable characteristic in the feathering or in the supraorbital comb (Pl. xvi., Figs. 3 and 4), or in any external part of the bird, by which the sex can be distinguished. In most Red Grouse, even in the vast majority, the confusion of sex is not possible, for it is a matter of common knowledge that for a great part of the year the cock and the hen are so wholly unlike one another as to make it difficult for any one who did not know the birds to believe them to be of the same species. Even in the summer months when the cock puts on a plumage closely simulating the breeding plumage of the hen, there is a difference in the general tone and colour, and confusion is not likely. But in the autumn and winter it is comparatively easy to mistake the sex of some individuals, for when the hen has put on her autumn plumage for the winter, and the cock has put on his winter plumage, certain individuals of opposite sex are then indistinguishable, even to the practised eyes of the experienced gamekeeper.

Generally speaking, the feathers of the head and neck give the best indication as to sex in the autumn-winter plumage. In the male the red colouring is, as a rule, far more uniform than in the female. In the male also there is, as a rule, an absence of black markings on these red feathers, except on the upper part of the head, on the crown, and nape of the neck. The cheeks are generally a clean bronze or chestnut-red colour; so are the feathers of the chin, throat, fore-neck, and upper breast, giving the bird a very rich uniform red colour all over the head and neck. In the hen, as a rule, the whole of the feathers of these parts are crossed by narrow black bars, which give her more of the mottled and broken colouring which the cock bird only begins to assume in the early summer when he puts on the first feathers of his autumn plumage.

The feathers of the chin are a very useful indication of sex from August to November, practically throughout the shooting season, for the chestnut-red feathers which can be found on the chin of the cock Grouse in every month of the year will be sought for in vain in the hen at this time. Even in December and January they are so imperfectly red as compared with the same red feathers in the male that one may almost say that red feathers are to be found on the chin of the hen only from February to July, when they become conspicuous on account of the contrast in colour with the increasing yellowness of the breeding plumage. These red feathers persist from her previous

autumn - winter plumage exactly as do the feathers of the lower breast and abdomen.

This persistence of winter-plumage feathers on the chin, lower breast, and abdomen is common to both cock and hen; but in the cock they remain, as a rule, until replaced by the following winter plumage, persisting throughout the autumn plumage change; whereas in the hen they are persistent only to June or July, and are entirely replaced during the autumn change. Even when the autumn plumage is put on, the yellow feathers of the preceding breeding plumage are almost always to some extent persistent, and they are to be found in the chin of the hen bird even though the throat and neck may be unusually red and therefore unusually like those of a cock bird.

From January to May there is no possibility, as a rule, of confusing the sexes. In June and July confusion is unlikely, but in August and onwards to December the differentiation of the sexes by the plumage is sometimes a difficult thing, and the best guide is the persistence of feathers of the preceding plumage such as occurs upon the chin in particular. We must recollect that the dominating plumage of the male is the winter plumage, while that of the female is the summer or breeding plumage.

In the autumn, especially from September and October onwards, there is the additional difficulty of distinguishing old birds and young.

“Young birds in July resemble the adult female in breeding plumage in their general colour, but the flank feathers of the adult plumage begin to appear about this time. By the month of November the young are generally not to be distinguished from the adults.” This quotation is from Mr Ogilvie-Grant.

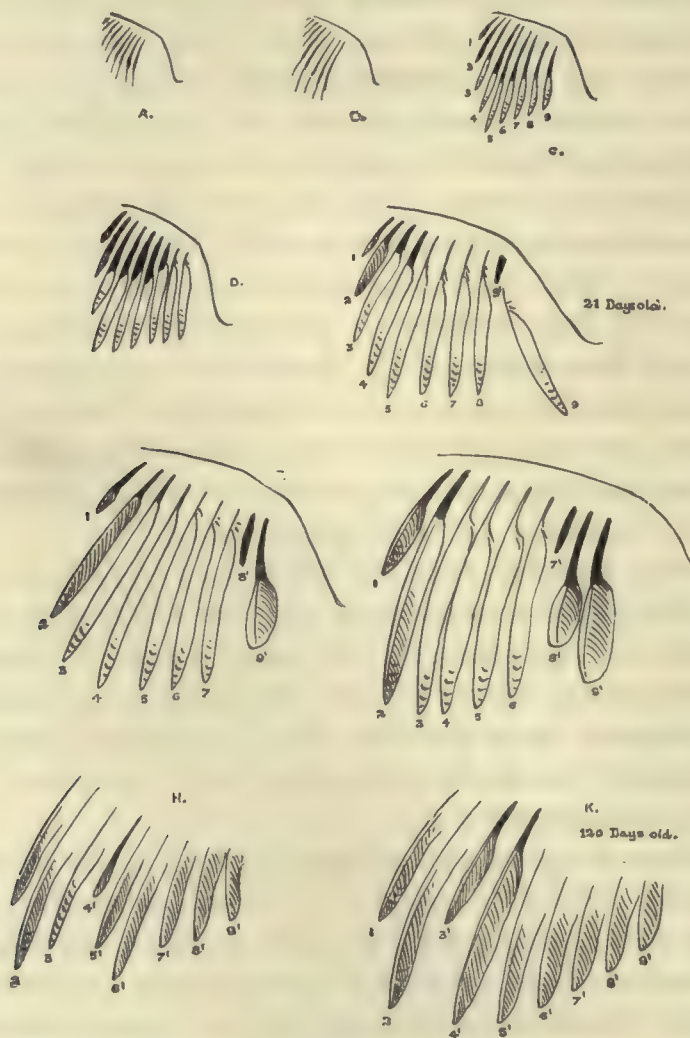
Distinction
between
old and
young
birds.

There is one sign of age in the majority of birds in the shooting season, if it has not become obliterated—namely, the mark across the claws of recent shedding. Very often one may find the nails or claws still adhering to the toes, though ready to drop off, so that a gentle application of force removes them like small caps, leaving the new shorter claws beneath, each marked by a groove where the old claw was attached. This groove persists often for some little time, and is an infallible sign that the bird is over a year old at least. Young birds of the year do not shed their claws, and therefore never have this groove.

Groove
on claw.

There is another method of determining a bird's age which is often used as a rough indication upon the moor, namely, to pull out the third primary

feather of the wing at its distal end. If blood can be squeezed from the quill it is considered as a sign that the bird is of the year. If no blood can be squeezed, and the feather is old and dry, it is considered as a sign that the bird is more than a year old.



Diagrammatic Representation of the Growth of Primaries in the Young Grouse.

This reasoning is based upon the following facts: When the chick produces its first set of primary wing feathers they are all very thin and weak, and soon become frayed out; they have rather narrow pointed ends, are blackish-brown, in colour mottled with incomplete buff bars. Nine of these little feathers can be

counted in series, and the weakest of all is the ninth counting from the distal to the proximal end. The diagrams on page 64 show very roughly the sequence of growth in the primaries of chick and pullet.

The growing power, as judged by the size of the root sheaths of these feathers, increases from the ninth distally, so that at one period of growth (F) the feather No. 4 is the longest, then a little later (G) No. 3, then still later (H) No. 2. But No. 1 remains permanently shorter than No. 2.

By the time Nos. 1 and 2 are approaching full growth, the weak chicken feathers Nos. 9, 8, 7, and so on have been shed, and in their place have appeared strong feather-roots growing strong, round-ended, uniform black primaries, instead of the weak, mottled, more narrowly pointed chicken primaries.

This shedding and replacement continues as far as No. 3 of the chicken primaries, but when No. 3 falls out Nos. 2 and 1 are found to have grown into such long and strong feathers as to fall into the series of new replacement feathers, and so they remain, now fully grown, and they can be recognised (K) by their more pointed ends having rather more of the buff markings on them than have the remainder of the primaries just grown from No. 9' to No. 3. No. 3, moreover, being the latest of the whole series of primaries to emerge, is for a time the shortest one; and, even when as long as No. 2, will be still the last one grown, and will therefore upon withdrawal produce blood at the quill end when squeezed between the finger and thumb.

This sign of blood in the quill of the third primary is not an infallible sign of youth, for it is evident that as soon as the feather finishes its growth the quill becomes as hard and dry and bloodless as all the others. The only indication will then be a slight difference in the shape and contour of the two last feathers as indicated above.

Moreover, in September it is easy to find birds obviously adult with claws attached but on the point of being shed, and having all the primaries moulted except the two most distal ones. The third then will be found to be a short feather actively growing, and if it is pulled out the growing root will be full of blood. Therefore not every bird that gives this sign is necessarily a bird of the year. The condition of the ends of the primaries, and especially of the two most distal feathers will, however, be a fair indication of age.

Another sign often used to test the age of a bird is the strength of the lower jaw. The weight of the bird is allowed to hang without support by

holding the tip of the lower bill only. The bone of an old bird's jaw easily stands this test, but the soft jaw of a young bird of three or four months cannot carry its weight, and the jaw either bends or breaks.

Lower bill. Yet another test often used is that of trying to crush in the skull with the finger and thumb; in the young bird the soft skull gives way readily, in the old bird it requires very considerable force.

Skull. In judging at a moment's notice whether a young Grouse chick which rises to the dogs on the 12th is of a shootable age and growth or not, the usual rule is probably as good a one as can be found—namely, that there should be a very clear view of black tail feathers before the young bird is fit to kill.

Tail feathers. It is only necessary, however, to look at a few young Grouse chicks of various ages to be convinced that more than a little of the black rectrices should appear before the bird is shot. Probably most sportsmen will be guided better by the strength of the bird upon the wing than by the black tail feathers, however clearly visible in a half-grown chick.

In dissection, the age of an old bird is apparent, perhaps as plainly upon the table as elsewhere. The fibrous tissues all toughen with age and use, and the bones become harder. The grits of the gizzard in an old bird seem to be larger and more worn into rounded pebble shapes, the reason for this has been discussed elsewhere.¹ The question, therefore, of deciding whether a bird is less than a year or more than a year old, is possible, but it seems almost impossible to judge more exactly of the age of an older bird by any sign to be discovered either externally or internally.

¹ *Vide* chap. iv. p. 95.

CHAPTER IV

FOOD OF THE RED GROUSE

By Edward A. Wilson and A. S. Leslie.

PART I.—OBSERVATIONS ON THE FOOD OF GROUSE, BASED ON AN EXAMINATION OF CROP CONTENTS.

DURING the period of the Inquiry the contents of several hundreds of loaded crops have been examined by the Committee with a view to ascertaining the various foods eaten by Grouse; the percentage compositions have been tabulated, as well as the total weight of food in the crops at the various hours of the day, and by these means the Committee have come to several unexpected conclusions.

Methods of
examina-
tion.

Table I. (p. 68) shows how the three hundred and ninety-nine specimens of crop contents examined are distributed as to locality and as to date, during the three years 1906, 1907, and 1908.¹ It is natural that by far the greater number should have been supplied during August and September; but the remainder are fairly evenly distributed.

Table II. (p. 69) is drawn up to show the average weight of the crop contents of birds killed at different hours of the day, from 6 A.M. to 6 P.M.

Time of
feeding.

In the last right-hand column of Table II. will be found a general average for the twelve months, and it will be seen from the figures given that Grouse feed from morning until night, but that full crops are more commonly found in birds killed in the afternoon and evening, both in winter and summer, than in the morning and forenoon.

When a Grouse is in health the gizzard invariably contains food undergoing a grinding process throughout the hours of sunlight, even in the longest

¹ In addition to the 399 crops tabulated some 1,100 other crops were examined—these were obtained mainly from diseased birds in April and May, and from shot birds in August and September.

summer day. The crop, it is true, is often found very full towards evening, and rarely so before noon; but this is only because in the evening the bird feeds more heavily in order to store up food for the hours of darkness, while

TABLE I.—CROP CONTENTS; MATERIAL EXAMINED.

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	
Aberdeen	1	...	1	2
Argyll	3	2	1	2	1	1	3	10	23
Arran	1	1	1	1	4
Ayrshire	2	5	7
Banff	2	2
Caithness	1	2	1	5	1	...	3	...	7	20
Dumbarton	1	1	3	1	3	6	12	1	5	...	33
Dumfries	2	2	2	...	2	4	2	2	1	...	2	5	24
Haddington	1	1
Inverness	7	5	3	1	3	38	15	1	...	9	82
Kincardine	1	...	1	2
Kirkcudbright	1	1	2
Lanark	1	1	2
Midlothian	2	...	1	...	1	3	7
Moray	1	...	2	1	2	6
Mull	1	1
Peebles	1	1	1	3
Perth	3	3	3	1	...	2	2	1	1	...	5	21
Ross	3	...	4	1	...	6	...	1	2	7	...	2	26
Roxburgh	2	1	1	5	...	9
Selkirk	3	3	1	7
Stirling	1	4	5
Sutherland	1	1	1	1	1	5
Wigtown	1	1
Cumberland	1	1	1	...	1	...	10	2	16
Derby	1	1	2	2	6
Durham	1	1	...	2
Lancashire	2	2
Northumberland	4	4	2	1	2	...	2	15
Westmorland	2	3	2	2	1	2	12
Yorkshire	1	6	5	7	2	4	7	1	3	36
Ireland	1	1
Wales	2	4	2	1	5	14
	33	39	33	30	16	12	12	67	44	27	15	71	399

Total number of crop contents examined = 399.

during the daytime he seldom eats more than the digestive processes can deal with at the time. Hence during the early part of the day the food passes rapidly from the crop to the gizzard and on to the digesting tracts of

the gut proper, and the crop is left almost empty. This has given rise to the view that Grouse only feed once a day, and that in the evening.

Heather (*Calluna vulgaris*), as is well known, is the ordinary food of the

TABLE II.—WEIGHT IN GRAINS OF CROP CONTENTS IN WHICH THE HOUR OF COLLECTION WAS GIVEN FROM APRIL TO NOVEMBER INCLUSIVE.

Hour of Collection.	Weight of Crop Contents of each Bird in Grains. (April to November.)	Weight of Crop Contents of each Bird in Grains. (December to March.)	Average Weight, in Grains.		
			Apr. to Nov. Average.	Dec. to Mar. Average.	Com- bined Average for 12 Months.
6 a.m.	1	10, 10	1	10	5½
7 „	8	No specimen	8	No speci- men	8
8 „	No specimen	20	No speci- men	20	20
9 „	1, 8	10	4½	10	7½
10 „	3, 18, 19, 4, 4, 20, 9	No specimen	11	No speci- men	5½
11 „	18, 2, 16, 27, 20, 14, 3, 13, 24, 40, 28, 36, 43, 34, 11	5	22	5	13½
Noon.	12, 14, 2, 11, 18, 6, 7, 15, 21, 7, 1, 6, 15, 24	120, 10	11½	65	38
1 p.m.	18, 36, 62, 29, 32, 2, 3, 5, 13, 13, 18, 12, 19, 0	No specimen	19	No speci- men	19
2 „	26, 45	70, 60, 20	35½	75	55½
3 „	50, 173, 98, 213, 334, 27, 7, 12, 17, 26, 18, 14, 2, 6, 8, 28, 52, 24, 48, 31, 1, 5, 68, 31, 32	110, 100, 80, 180, 358, 200, 369, 50, 380, 250, 320	53	217	135
4 „	15, 1, 4, 4, 246, 50, 17, 32, 50, 43, 50, 46, 8, 4, 2, 43, 3	339, 429, 239, 369, 429, 599, 280, 280	36	370½	208½
5 „	8, 1, 1, 2, 1, 254, 66, 18, 5, 32, 23, 17, 7, 23	150, 210, 200	32½	186½	109½
6 „	37, 93, 114	10, 349, 290, 20, 409	81	214	147½

adult Red Grouse. But twenty or thirty other plants are also eaten, often in great quantities, and it is a well ascertained fact that Grouse that have never set eyes upon a sprig of heather will live and flourish for years.

Yet the importance of heather in building up the birds for the approach of winter cannot be exaggerated, and there is little doubt that in a bad heather year all the young birds suffer, while even in a good heather year the later broods will be permanently handicapped as regards physique and disease-resisting power if they have missed the best food months.

The most noteworthy fact brought out by Table II. is that Grouse appear to require a larger quantity of food in the winter months from December to March, than in the spring, summer and autumn months from April to November.¹

It is, of course, true that in a bad heather year Grouse may find substitutes for their staple diet. Of these substitutes blaeberry is undoubtedly the most valuable, as may be seen by reference to Tables III. and IV.;² but in many districts blaeberry does not grow upon the moors, and in no case is it so reliable a winter food as good heather. Other substitutes for heather are rush-heads, crowberry, bog myrtle buds, seeds of *P. tormentilla*

TABLE III.—SHOWING THE PERCENTAGES OF VARIOUS FOODS FOUND IN CROP CONTENTS OF GROUSE FROM APRIL TO NOVEMBER INCLUSIVE.

	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.
Calluna (Heather) shoots, fresh and green . . .	47	69½	82	31½	59½	63½	31	24
Calluna (Heather) shoots, brown but living . . .	46	12	0	21½	1	0	11	15
Calluna flower-buds, flower and seed-heads . . .	0	½	0	0	5½	16½	28	33
Blaeberry (<i>V. myrtillus</i>), stalks and leaves . . .	4	6	6	20	0	4½	9	22
Various, including Erica, Crowberry Fern, Sorrel, etc.	3	12	12	27	34	16	21	0

fern leaves, bog cranberry leaves, flowers of *Erica tetralix* and *Erica cinerea*, moss spore capsules, sheep sorrel leaves and seeds, insects, and oats. On pp. 83-87 will be found a list of the vegetable foods eaten from time to time by the Red Grouse, with illustrations of some of the plants referred to.

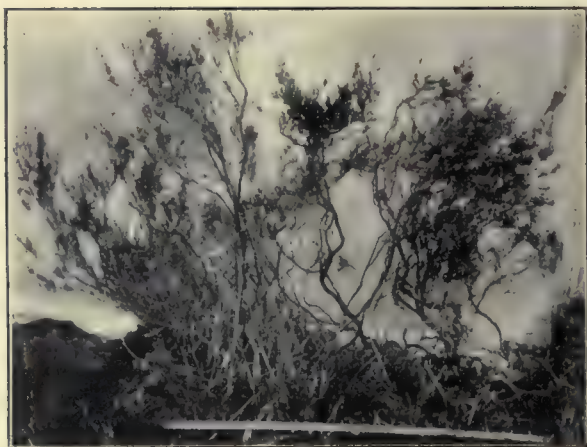
The summer substitutes for heather, while interesting as showing the wide range of the Grouse's diet when many varieties of food are available, cannot be considered of great importance to the health of the adult bird, for if the

¹ Vide also p. 79.

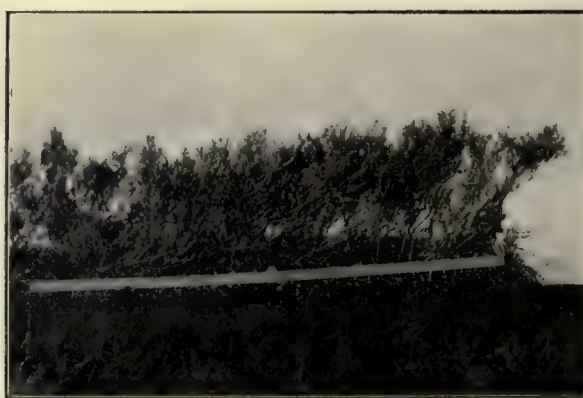
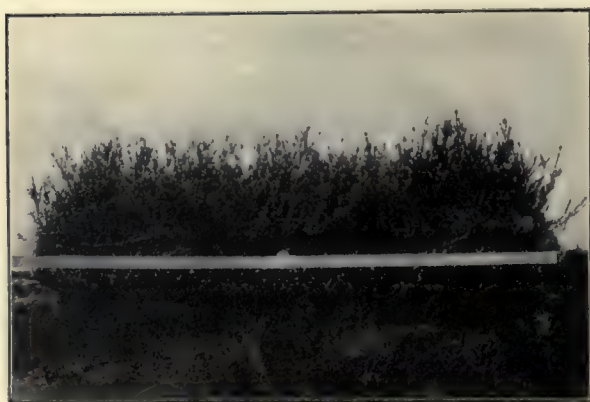
² Vide pp. 76, 79 and 80.

PLATE XXIII

TYPES OF HEATHER.



Old Heather valueless as food for Grouse.



Young short Heather valuable as food for Grouse.

heather is good, and the supply sufficient, the stock will be well nourished and healthy, even on a moor where there are no berries or other miscellaneous kinds of food.

Heather then is the essential basis on which the Grouse depends, and the importance of the plant is so great that it may be permitted to give a short description of the phases through which it passes during the seasons of the year.

Beginning with the months of early spring, it will be seen from Table III. that in April the Grouse's diet consists of an equal quantity of fresh green heather and of brown "winter" heather. The former is more nutritious than the latter, but even the brown winter heather is better than nothing, and is to be distinguished from withered dead heather which Grouse never eat.

The fresh green heather so desirable for the food of Grouse does not necessarily represent the young shoots of the spring growth, for these do not generally appear till May, but rather the evergreen foliage which the plant carries upon its lower branches throughout the winter. No one who casually examines a Grouse-moor in midwinter can realise that the dull brown weather-beaten scrub conceals on its more sheltered twigs a luxuriant growth of vivid green shoots: these green shoots are far more numerous on short close heather than on the long overgrown heather so common on many moors, for as the plant increases in height it becomes more open in its growth and more susceptible to the blighting effects of frost and cold winds.

In cases where the heather has attained a height of several feet the shelter is so greatly reduced that it is sometimes difficult to find any green shoots at all in winter unless the weather has been unusually mild; such long overgrown heather is of practically no value as winter food for Grouse (*see* Pl. XXIII., Fig. 1). This type of long and apparently luxuriant heather is very common on the west coast of Scotland, and in many districts in the central Highlands, and probably accounts for the fact that these districts carry a comparatively small stock of Grouse. In other districts the heather seems to have developed a short, close habit of growth—to the uninitiated it would appear to be stunted and poor; yet it is in the districts where this dwarf type of heather is common that Grouse appear to thrive in the largest numbers. The hills are covered with a close carpet of vegetation having a smooth level surface which may be compared to a well-clipped yew hedge—this level surface forms a canopy of shelter from frost,

Winter
heather.

Short
versus long
heather.

Dwarf
type of
heather.

while the stems of the heather are so short and stiff that they are little affected by the wind. If this type of heather is examined, it will be found that immediately below the weathered canopy there is a rich growth of bright green shoots even in the most severe winter (*see* Pl. XXIII., Fig. 2).

There is no doubt that it is on the moors which have a large proportion of this short, close-growing heather that the largest stock of birds can be carried over the winter. But it is only on a special class of ground that this type of heather is found to grow naturally; it is usually associated with dry, hard soil, good natural drainage, a rocky subsoil, and only a shallow layer of peat on the surface; it is uncommon in districts with a heavy rainfall.

Even on the best ground there is a tendency for the heather to grow too long and bushy; but this tendency can fortunately be controlled by artificial means. In another part of this Report the subject of heather burning is fully described,¹ and it is only necessary here to state that, for purposes of food, heather ceases to have any value after it has been allowed to become rank.

With the advent of May comes a great change in the condition of the heather plant. In this month every twig breaks out into green shoots, even the oldest and most ragged stick heather will produce young growth of the kind most valuable as food for Grouse; but it is now too late for this tardy recovery to be profitable, for the days of famine are past, and there is sufficient food to feed ten times as many birds as there are upon the ground. Even in this month of plenty, however, the close, short heather of from 4 to 8 inches in height is superior to the straggly forest of overgrown plants, for there is an ever present risk of a late spring frost, when the tender young shoots will require all the shelter they can get.

The appearance of the young growth is marked by an immediate change in the diet of the Grouse. On referring again to Table III., it will be seen that the consumption of fresh green heather shoots rises suddenly to 69½ per cent., while that of the dry winter heather drops to 12 per cent. At the same time the proportion of miscellaneous foods is more than doubled, owing doubtless to the fact that every moorland plant is throwing off its winter sleep and bursting into appetising young buds.

Just as the first flush of early pasture is more nourishing than the later growth, the first heather shoots of spring probably contain a larger percentage

¹ *Vide* chap. xviii. pp. 392 *et seq.*

of nutritive food than at any other time of the year, and it is doubtless due to this cause that Grouse make such rapid growth in size and strength between the date of hatching in May, and the opening of the shooting season some ten or twelve weeks later. Young growth very nourishing.

It is in the month of May also that the young heather plants first begin to appear on the black ground, where the old heather has been burned. The length of time that elapses between the date of burning and the growth of the new heather varies. If the roots are not too old, and have not been destroyed by the fire, the new growth will spring from them within a year; on some ground this always occurs. If, however, the roots have been burnt out, or are too old to send forth new shoots, the ground must lie waste for years, until a fresh growth of heather springs from wind-blown seed or from the seed lying dormant in the soil or blown on to it.¹ Growth of young plants.

It is usual to suppose that the first shoots of the young heather as they appear above the ground are greedily eaten by Grouse. Observation has shown that this view is not strictly correct, for the adult birds will never feed on the immature plant so long as they can find plenty of close-growing heather of the type described on p. 72. This is fortunate, for otherwise the first growth might be very severely checked on a moor carrying a heavy stock of birds. Sheep, on the other hand, are very fond of the tender young shoots, and are often most destructive to seedlings which have not had time to secure a firm roothold. Adult Grouse do not eat seedling heather.
Sheep do.

While the adult Grouse does not eat the very young heather, there is no doubt that the chicks prefer it to the shoots of the more mature plant; but the amount eaten by them in the days of their infancy is so small that they cannot make any material impression on the growth of the plant. So do Grouse chicks.

In June there is a continuance of the favourable conditions which commenced in May. It will be seen by reference to Table III. that in this month the consumption of fresh green shoots of heather rises to 82 per cent., while that of brown winter heather drops to zero. Heather in June.

In July the consumption of heather drops to its lowest for the year—only 53 per cent.; this is doubtless partly due to the ripening of blaeberrries which occurs in this month. The consumption of blaeberry stalks and leaves has risen to 20 per cent., while the quantity of berries eaten is In July.

¹ *Vide* chap. xviii. p. 400.

shown by the increase of "various" to 27 per cent. The unexpected increase in the consumption of brown winter heather is puzzling, but might be accounted for by an abnormal period of cold weather or blighting wind causing a "set back" in the new growth, and driving the birds to feed more largely on the old shoots. This view is supported by the fact that the birds have also eaten an abnormal quantity of blaeberry stalks and leaves, whereas in the following month, when the heather has presumably recovered from its temporary blight, the consumption of brown winter heather and blaeberry leaves and stalks drops at once from 47 per cent. to 1 per cent. The figures for July shown in the Table are probably exceptional, and do not represent the normal proportion of foods eaten in that month; but they are interesting as showing the elastic manner in which the Grouse can adapt himself to varying conditions.

In August the figures for the consumption of heather appear to have become normal, and the fact that this is the great berry month of the year is shown by the increase of "various" to 34 per cent., the largest amount in any month. Berry feeding is, of course, irregular, for berries only grow in certain localities, their consumption cannot therefore be gauged by the examination of specimens obtained from moors where no berries are obtainable. Berries are not an essential item in the diet of the Grouse; but it is well known that where they are to be obtained Grouse will flock to them in large numbers, often deserting the heather altogether for a while, and congregating in vast packs upon the berry ground. The blaeberry fruit does not as a rule grow in such profusion as that of the clusterberry or Scottish cranberry, and does not seem to be so attractive to the Grouse, though its leaf and bud are much more generally eaten at all times of the year.

The August figures are interesting as showing the first indication of heather blossom in the diet. First in the bud, afterwards in full bloom, and lastly in the form of fully ripened seed, the flower of the heather is an important item of food. There is an old saying that when the "stoor" (*i.e.*, pollen dust) is on the heather in August a good Grouse season is sure to follow, and the experience of the Committee tends to confirm this belief. In a year when the bloom is early and luxuriant the pollen rises in clouds when disturbed, covering boots and gaiters with a soft yellowish dust, and sometimes even interfering with the breathing of the dogs. This condition is usually followed by a fine harvest of well-ripened heather seed, and the importance

Excep-
tional char-
acter of
July
figures.

In August.

Berries.

Heather
flowers
and seeds.

of heather seed as a form of food may be seen at a glance from the figures given in Tables III. and IV.

It is often stated that in seasons when the corn has ripened well and early, the stock of Grouse in the following spring is healthy and vigorous, and the breeding season a good one; from this it has been argued that the same weather which has resulted in a good crop of grain has also produced a good crop of heather seed. This factor too may have something to do with the difference in the numbers of Grouse which moors in different parts of the country are capable of carrying. It is well known that the number of Grouse on a moor does not depend upon the area of heather land, for in the thinly-stocked moors of the west of Scotland the heather growth is stronger than in the south of Scotland, where in many districts there is a larger stock of birds. Even in Yorkshire, Lancashire, and Derbyshire the ground does not appear to be better suited for the growth of heather than in Scotland, yet in these counties the stock of birds is proportionately much greater. The difference is partly to be accounted for by the fact already noted, that the heather in the north of England is of a better quality, that is to say with many more stalks to the acre, than the rank growth of the west of Scotland, but it has also been suggested that in the former country the normal weather conditions are more favourable to the ripening of the heather seed. Again, in Caithness, where the grain always ripens well on account of the long hours of daylight in the summer months, the stock of birds which the ground can carry is unusually large.

A good grain year usually a good heather year.

A good grain district usually a good Grouse district.

In September, October, and November, the tendency to revert gradually from summer to winter diet is well exemplified by the figures in Table III. Throughout these three months the consumption of the heather seed increases steadily, while "various" drops from 16 per cent. in September to 6 per cent. in November. In October we find the item of "brown winter heather" reappearing in the list, and in November we have a sudden increase in the consumption of blaeberry stalks and leaves, due probably to some temporary check suffered by the heather similar to that indicated by the figures for July.

In September, October, and November.

Turning now to Table IV. (p. 76) we find that in the four winter months the diet becomes more restricted. "Various" practically disappears, and its place is taken by a larger quantity of heather shoots, while heather seeds and blaeberry stalks still keep their place in the list.

Winter food.

One or two points are worth noting. In the first place, the sudden drop in

the consumption of heather seed from $20\frac{1}{4}$ per cent. in January to $2\frac{1}{2}$ per cent. in February and $2\frac{1}{3}$ per cent. in March is interesting as showing that once the seed has fallen to the ground it is no longer eaten by Grouse, though it may be valuable for the reproduction of the plant.

Heather
seed not
eaten after
January.

TABLE IV.—SHOWING THE PERCENTAGES OF VARIOUS FOODS FOUND IN CROP CONTENTS OF GROUSE FROM DECEMBER TO MARCH INCLUSIVE.

	December	January	February	March
<i>Calluna</i> (Heather) shoots . . .	59 $\frac{3}{4}$ per cent. } 86 $\frac{3}{4}$	64 per cent. } 84 $\frac{1}{2}$	75 $\frac{1}{2}$ per cent. } 78	97 per cent. } 99 $\frac{1}{3}$
<i>Calluna</i> (Heather) seed-heads . . .	27 " (more than $\frac{1}{3}$ ripe)	20 $\frac{1}{4}$ " (more than $\frac{1}{3}$ ripe)	2 $\frac{1}{2}$ " }	2 $\frac{1}{3}$ " }
Blaeberry stalks and buds (<i>Vaccinium myrtillus</i>) . . .	10 per cent.	13 $\frac{1}{4}$ per cent.	15 "	...
Various, including Cowberry leaves (<i>Vaccinium vitis-idaea</i>), Bog Cranberry leaves (<i>Vaccinium oxycoccus</i>), Crowberry leaves (<i>Empetrum nigrum</i>), <i>Erica</i> , sorrel, fern, and other green leaves	3 $\frac{1}{3}$ "	2 $\frac{1}{2}$ "	7 "	$\frac{2}{3}$ "

Another point is that both in this and the preceding Table, the figures relating to the consumption of blaeberry stalks and leaves are misleading because they are the result of averaging the crop contents of a large number of birds—many of them sent from localities where blaeberry is unknown. Were the crops of individual birds recorded it would be found that those coming from moors where blaeberry is common would show almost as large a consumption of that plant as of heather. Blaeberry forms as much as 30 per cent. of all foods taken by Grouse in Derbyshire, 22 per cent. in Yorkshire, and 11 per cent. in Inverness and Dumfriesshire, and very little in any of the other counties.

In special cases these averages are departed from, especially when the heather crop has been a failure. Thus some December specimens from Lancashire showed the remarkable average of 80 per cent. of blaeberry stalks and buds, with only 17 $\frac{1}{2}$ per cent. of heather shoots and 2 $\frac{1}{2}$ per cent. of heather seed, but in this case the heather-seed crop in Lancashire was reported as very bad. In the same year the heather-seed crop in Peebles and Merioneth was reported as exceptionally good, and the December specimens from both these counties showed the proportion of 50 per cent. of heather shoots and 50 per cent. of heather seed, but no blaeberry.

Blaeberry
eaten
largely
where pro-
curable.

Probably the consumption of other foods, which are classed under "various," and have already been enumerated, varies in the same way chiefly with local relative abundance, as, for example, in Perthshire, where "various" rises to 53 per cent.; Ayrshire, where it reaches 47 per cent.; and Derbyshire, where it reaches 40 per cent. of all foods taken.

Individual taste plays a large share in the food statistics of Grouse. One may find, for example, one bird eating largely of fern leaf, another of bog myrtle buds, another of nothing but rush heads or *tormentilla* seed. In one case, where two birds were killed with a "right and left" in a Grouse drive it was found that one had filled his crop with heather shoots, the other with blaeberry leaf buds, yet both birds had come off the same beat. Occasionally one finds that even an adult bird has eaten scores of small black gnats. The flower of *Calluna* is varied occasionally by the flower of *Erica tetralix*, or ripe cluster berries, or spore-capsules of several mosses, or leaves of the cloudberry.

The interest of Table IV. centres on the first item, "Heather Shoots," for the figures prove conclusively, if proof were required, that, except on favoured moors where blaeberry abounds, heather shoots and nothing but heather shoots constitute the diet of the Grouse during February and March—the fact that the February column shows 7 per cent. of "various" was due to one bird's crop being almost entirely filled with crowberry leaves, a quite unusual diet; the "various" consumed by other specimens examined for that month only amounted to $\frac{1}{3}$ per cent.

Heather
shoots the
sole diet
in Febru-
ary and
March.

It is obvious, therefore, that in February, March, and April the question of food becomes a critical one, for if the heather fails the Grouse must suffer either by direct starvation, or what is much more dangerous, by being forced to crowd too closely on to the few small areas where good winter heather is to be obtained.

Although we have no evidence from any one of the hundreds of Grouse crops examined that true frosted heather is ever eaten, the heather which actually filled the majority of the winter crops varied greatly in its value as a food. It could often be seen that the birds had been hard put to it to fill their crops at all, perhaps from stress of weather, or possibly because of excessive or deficient burning or an overstock of sheep, or for some other less obvious reason.

The mere fact that the crops of many birds contain old heather is enough

to prove that birds sometimes find great difficulty in collecting a meal of wholesome food. The vast majority of winter crops contain, as we have already said, good dark green or dark reddish brown winter heather, sound wholesome food with a minimum of dead woody tissue. But now and again one finds a crop full of old woody growth of which the food value must be very small. And though the cause of this may sometimes be that the bird is a weakling and has been driven off the better feed to live upon whatever it can find elsewhere, yet this inferior food is sometimes found in the crop of a bird which is evidently no weakling. It may then be due to the fact that the moor has been left long unburned, and that all the heather within reach is old and rank. Or the moor may have been over-burnt from every point of view except that of the grazing tenant. In such a case large tracts of young heather are burned again and again, often by runaway fires, to bring the land to grass and kill the heather. In this the grazing tenants of parts of the borderland and of the north of England have been very successful, and heather in many places is a thing of the past, the moors being now almost all white land. Scattered through this, where the tussocky grass has had its way for many years, is a thin growth of useless straggling heather of little value as food for bird or beast.

For the purpose of drawing up Tables III. and IV. two hundred and eighty-seven specimens of Grouse were examined, and the specimens were fairly evenly distributed over the months from April 1906 to March 1907. The specimens represented birds from no fewer than twenty-seven different counties, so that the results may be regarded as conclusive, so far as concerns the particular period under review.

In case, however, of the period selected being abnormal, Table V. (p. 79) was prepared to show the crop contents for two complete years, viz., 1906 and 1907. In this Table the figures for the corresponding months are placed together, and an average is struck for each month. It will be seen that these averages show the same general tendencies as are seen in the former Tables, and confirm the view that the figures given in Table III. for July and November 1906 were abnormal, and probably due to exceptional circumstances.

The total number of specimens examined for the purpose of drawing up Table V. was four hundred and thirty-six, including the two hundred and eighty-seven already included in Tables III. and IV.; but in 1907 specimens were

not quite so well distributed as in the earlier period. This remark specially applies to May, June, and July 1907, when only one specimen was received for each month as against a monthly average of fifteen in 1906.

TABLE V.—COMPARISON OF MONTHLY AVERAGES OF CROP CONTENTS COVERING TWO YEARS.

		Jan.	Feb.	Mar.	Apr.	May.	Jun.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Calluna</i> heather shoots	1906	64	75½	97	93	81½	82	53	60½	63½	42	39	54
	1907	89	72	81	64	100	100	95	38	63	51	70½	59½
	Av.	76½	73½	89	78½	90½	91	74	49½	63½	46½	54½	56½
<i>Calluna</i> heather flower and seed-heads	1906	20½	2½	2½	0	½	0	0	5½	16½	28	33	23
	1907	10	9	2	0	0	0	0	14	21	24	19½	27
	Av.	15½	5½	2½	0	¼	0	0	9½	18½	26	26½	25
Blueberry stalk, bud, and leaf	1906	13½	15	0	4	6	6	20	0	4½	9	22	21
	1907	½	19	15	21	0	0	0	12	0	1	10	10
	Av.	6½	17	7½	12½	3	3	10	6	2½	5	16	15½
Various	1906	2½	7	¾	3	12	12	27	34	11	21	6	2
	1907	½	0	2	15	0	0	5	36	16	24	0	3½
	Av.	1½	3½	1½	9	6	6	16	35	13½	22½	3	2½

The results of this Table have also been given in the form of a chart for purposes of comparison.¹

The strain upon the vitality of the Grouse in the winter months is intensified by the fact that a greater bulk of food is required by each bird per day than is required during the summer.

But few would have rated it at five times the value, and yet, from a comparison of the afternoon crops of the winter with those of the summer, this appears to be the case. Thus the average weight of food found in a Grouse crop from December to March, between 3 P.M. and 6 P.M., is 250 grains, whereas the average weight of food found in a Grouse crop from April to November, between 3 P.M. and 6 P.M., is only 50 grains.

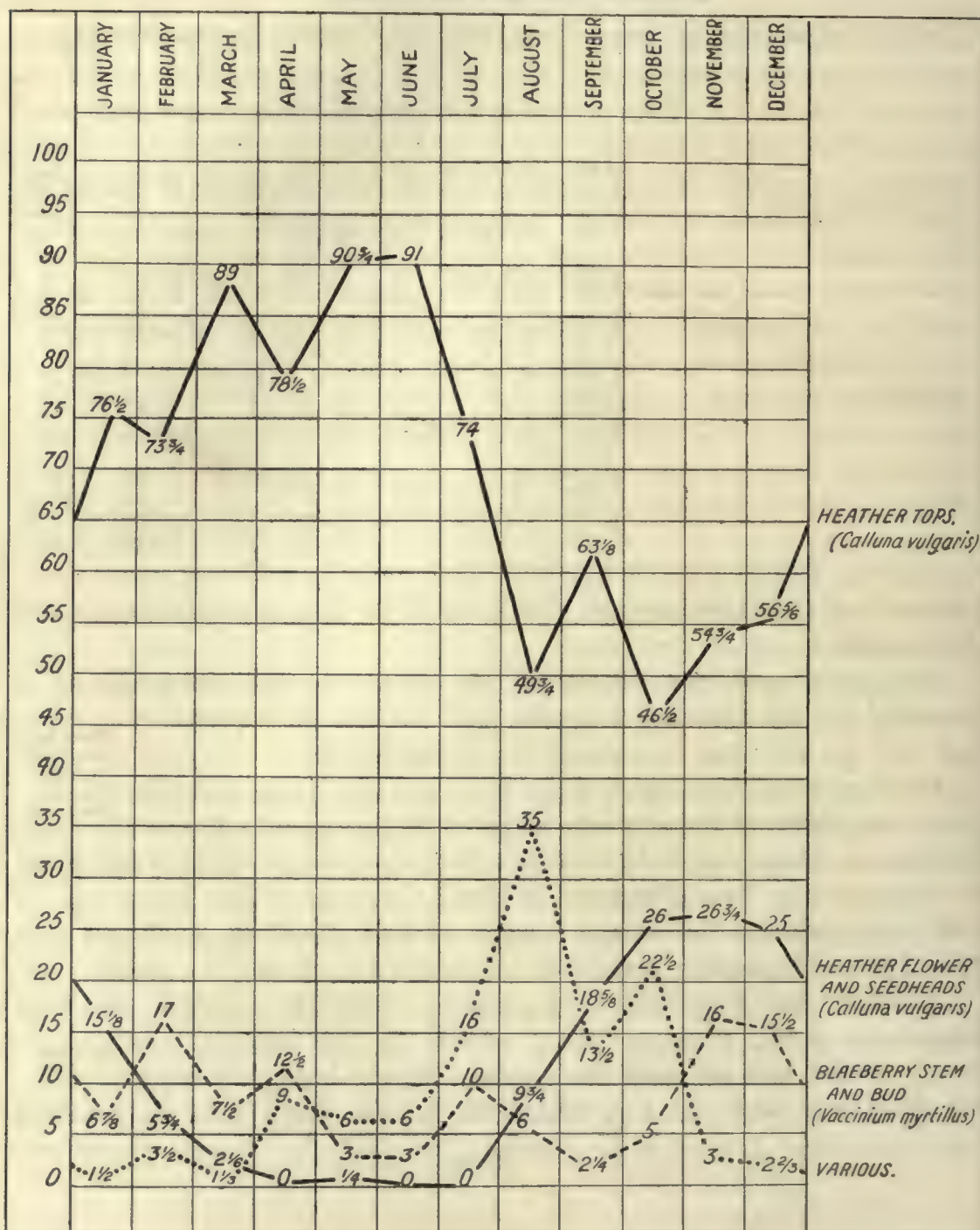
The fact that more food is required in winter to maintain the body temperature would, of course, partly account for this increase, even if the heather had the same food-value. But as heather certainly has an inferior food-value in winter, the amount taken must be increased

More food
required
in winter
than in
summer.

Reasons
for this.

¹ Vide p. 80.

CHART SHEWING
PERCENTAGE CONSUMPTION OF VARIOUS FOODS EATEN EACH
MONTH BY THE RED GROUSE



in a far greater proportion. No doubt the necessity for provision during the longer hours of night-time has some effect in the overfilling of the crop in winter, but this would not account for crops being heavier in March, when the days are comparatively long, than in November when they are short.

The interesting fact remains, and is amply proved by the figures, that more food is required by the Grouse in winter than in other seasons of the year; and as in winter the proportion of *Calluna* to all other foods is as seven to one, it is obvious that a very great advantage accrues to a Grouse on a moor in which young and comparatively nourishing heather is abundant during the winter months, *i.e.*, on a well-burned moor, well covered with young heather of a varying number of seasons' growth.

To put this conclusion in other words; whereas in summer a certain area of heather will support a bird comfortably, many times this area will be required for the same bird in the winter, so that the capacity of a moor, as regards the question of stock, must be gauged mainly by its Grouse-feeding value during the winter months.

If we consider this generalisation with reference to moor management we shall see that a moor carrying its full tale of birds in the summer becomes automatically and unavoidably overstocked in the winter unless the stock is heavily reduced by shooting, for not only is there less food available, but the birds require a much larger quantity of food to keep them in health.

Migration of birds in winter obviously complicates the question. In the case of a moor on high ground, which often loses all its birds in winter, probably natural conditions regulate the stock of birds automatically during spring and summer. But on the adjacent low-lying moors Effect of migration. the case is more serious; for the ground has to supply not only more food than is needed for its own stock in summer, but in addition an increased seasonal demand made upon it during the winter months by hundreds of undesirable immigrants from the higher ground. Such low-lying moors must always run the risk of being dangerously overstocked in the winter.

In certain parts of the country oats form a regular seasonal change in the dietary of Grouse, and this form of food must now be considered.¹

Very few birds with corn in any part of the alimentary canal were submitted for examination; but so far as these specimens show, oats are an unsuitable form of food for Grouse. As is well known, Grouse often visit the

Oats.

¹ *Vide* also chap i. p. 25, and chap. viii. pp. 178-180.

stubbles and corn-stooks in very large packs in the autumn—in September, October, or November, according to the season and locality. They seem to know that they are out of place, and finding themselves with a wealth of food all round, away from their normal surroundings, are eager to fill themselves as full as possible in a very short space of time, aware, by instinct or experience, that they may be disturbed at any moment. One consequence is, as the examination of birds has shown, that they eat as much husk as grain, instead of picking and choosing as Partridges do, in a quiet and leisurely manner. This difference in the crops of Grouse and Partridges that have been feeding on the same ground is very noticeable. The one is filled to repletion with indigestible and exceedingly irritating husks and a comparatively small amount of grain, while the other (the Partridge's crop) contains grain only.

The result in the Grouse is that the whole alimentary canal, from one end to the other, is soon in an irritable and inflamed condition. The gizzard does what it can to work up the husks and grain into a milky paste, but the microscope shows that this paste is to a large extent composed of siliceous spicules and small spines of an almost glassy hardness. This damages the delicate mucous lining of the intestine. The result of the passage of this irritating food is, first, an extra flow of digestive juices, secondly, an increased activity on the part of the walls of the intestine, both as to movement (peristalsis) and secretion from the stimulation produced by this form of food. Thirdly, comes a point at which mucus is thrown out in large quantities to protect the gut, and this continues and increases until the actual cells themselves are shed, and the protection breaks down. Finally, the intestine becomes inflamed to the extent of ulceration, and this state will continue and increase so long as the cause continues to act.

Such irritation to the intestine of even a healthy Grouse, which already has to deal with worms of at least two kinds, is bound to have an evil effect if continued for any length of time; moreover, in places where the corn is left out owing to bad weather, or for other reasons, there is the additional aggravation that the birds may be filling themselves with wet and sour grain, not one whit the less irritating as regards the husk, which cannot be softened by wet; and no doubt the consequence of this is in some seasons noticeably bad.

Corn in moderation is probably not unwholesome as a food, and were it

possible to feed one set of Grouse with clean grain, and another with such stuff as the birds pick up for themselves on the stubbles, there is no doubt that the former would rapidly improve in condition, and the latter go steadily downhill. Such an experiment is not practicable.

To recapitulate, the following may be given as a fairly accurate account of the monthly dietary of the Red Grouse for the year:—

January, *Calluna* shoots (64 per cent.) and *Calluna* seed-heads (27 per cent.).

February, *Calluna* shoots (75 per cent.) and the stalks and buds of blaeberry and leaves of cowberry.

March, *Calluna* shoots (97 per cent.) and blaeberry stalks and buds.

April, *Calluna* shoots (93 per cent.) and very little besides.

May, *Calluna* shoots (82 per cent.) and rather more "various."

June, *Calluna* shoots (82 per cent.) and "various."

July, *Calluna* shoots (53 per cent.) and an increasing amount of "various."

August, *Calluna* shoots (60 per cent.) and some *Calluna* flowers and "various."

September, *Calluna* shoots (63 per cent.) and 16 per cent. of *Calluna* flowers and "various."

October, much less (42 per cent.) of *Calluna* shoots, and nearly 30 per cent. of *Calluna* flowers, and some "various."

November, still less (39 per cent.) of *Calluna* shoots, and 33 per cent. of *Calluna* flowers and seed-heads, and the rest "various."

December, a rise in *Calluna* shoots to 60 per cent., but still 27 per cent. of *Calluna* seed-heads.

LIST OF VEGETABLE FOOD EATEN FROM TIME TO TIME BY THE RED GROUSE

Calluna vulgaris, the staple food of Grouse, is known generally as Heather. Grouse eat the shoots, flowers, and seed-heads. See Pl. xxiii., p. 71.

Vaccinium myrtillus, Blaeberry, Blueberry, or Blue Whortleberry. Grouse eat the stem, buds, flowers, and berries. See Pl. xxiv., p. 86, Fig. 1.

- Vaccinium oxycoccus*, Bog Cranberry. The leaf and the berry are sometimes eaten. See Pl. xxiv., p. 86, Fig. 2.
- Vaccinium vitis-idaea*, Red Whortleberry, Clusterberry, and (in Scotland) Cranberry. Leaf and berry are eaten. See Pl. xxiv., p. 86, Fig. 3.
- Arctostaphylos uva-ursi*, Red Bear Berry. See Pl. xxiv., p. 86, Fig. 4.
- Rubus chamaemorus*, Cloudberry, or (in Cumberland) Noops. The leaf is eaten, and so are the berries. See Pl. xxv., p. 87, Fig. 1.
- Empetrum nigrum*, Crowberry, Crakeberry or Lingberry. The top shoots, tight leaf buds, and berries are eaten. See Pl. xxv., p. 87, Fig. 2.
- Erica cinerea*, Purple Bell Heather. The flower alone is eaten, but while it is out it is eaten in fair quantities. See Pl. xxv., p. 87, Fig. 3.
- Erica tetralix*, Cross-leaved Heath. Flower-heads are eaten in quantities, but leaf-shoots are avoided. See Pl. xxv., p. 87, Fig. 4.
- Salix repens*, Dwarf or Creeping Willow, a low, straggling shrub from 2 inches to 1 foot in height. Foliage and young shoots more or less silky white. The plant has small oblong leaves, and bears small catkins in spring, followed by silky seed vessels. Found on sandy ground. Where it occurs the leaves and young shoots are greedily eaten.
- Myrica gale*, Bog Myrtle, or Sweet Gale, an erect shrub, 2 or 3 feet high, fragrant when rubbed. It has long, narrowish pointed leaves, slightly toothed near the tip, and often downy beneath. It bears small catkins before the leaves are out. Always found in boggy places. The buds are eaten in winter and early spring, but sparingly.
- Eriophorum*, Cottonsedge or "Cotton Grass," two or three species of similar habit. A rush-like plant, bearing in summer, after the flowering period, conspicuous, white, cottony tufts, either solitary or in clusters of two or three or more. Grouse are very greedy for the flower of this plant in spring, and the tender shoots are also said to be useful when they first appear. The plant is then known by gamekeepers as "Blackhead" or "Mossdrop." It is found in marshy ground.
- Rumex acetosella*, Common Red or "Sheep" Sorrel. A slender plant, from 3 or 4 inches to 1 foot high, often turning red. It has long, more or less arrow-shaped leaves, very acid to the taste. The

red-tinged green flowers are in terminal clusters on an erect stem, and are seen from spring to autumn. The plant grows in dry pastures, and on open heaths. The seeds are greedily eaten.

Juncus squarrosus, Heath Rush, a small-rush about a foot high, growing in drier situations than most rushes. The flower- and seed-heads are very freely eaten.

Luzula campestris, Field Wood Rush, a small rush with soft, flat, grass-like leaves, fringed with silky hairs. It grows in dry places. The flower- and seed-heads are eaten.

The following additional list of plants, upon which Grouse are said to feed, is given in a pamphlet on "The Improvement of Grouse Moors," by the Rev. E. A. Woodruffe Peacock, who has examined the contents of many crops and gizzards of the Grouse.

Potentilla tormentilla, Tormentil.

Trifolium minus, Suckling Clover.

Galium saxatile, Heath Bed-straw.

Pedicularis palustris, Marsh Lousewort.

Pedicularis sylvatica, Heath Lousewort.

The seeds of the following plants are greedily eaten, and are most useful as late autumn and winter food:—

Alopecurus myosuriodes, Mouse-tail Grass.

Molinia cærulea, Purple Melio Grass.

Atriplex patula, Common Orache.

Cerastium triviale, Chickweeds and other moor cerastia.

Polygonum aviculare, and *P. persicaria*, Persicaria, and Knot Grasses of all species. The flower-heads are also eaten.

Viola lutea, Yellow Violet.

Pteris aquilina, Bracken Fern.

In their season, too, Grouse are very fond of capsules of the moor mosses, such as the Great Golden Maidenhair Moss (*Polytrichum commune*), and the smaller fungi.

For the purpose of reference the following plates and detailed descriptions are given of some of the moor plants most commonly confused on account of the variety of names by which they are known.

PLATE XXIV

FIG. 1

The BLAEBERRY (*Vaccinium myrtillus*), known also as the Whortleberry, Bilberry, Whinberry, Blueberry, or "Whorts" in various districts, a low branched shrub 6 to 18 in. high, growing often in large green patches. The flowers, which appear in April, May, or June, are flesh-coloured, and the berries, which are black with a purple bloom, ripen in July and August; they are agreeable to the taste.

FIG. 2

The CRANBERRY (*Vaccinium oxycoccos*), known also as the Bog Cranberry, Mossberry, Moorberry, or Fenberry, a very low plant with a prostrate, straggling, slender stem and small leaves. It is found creeping on the surface of the moss in boggy places. The flowers, which appear in June, July, or August, are solitary and bright red, and the dark red fruit is pleasant to the taste. This berry is common in many parts of England, but is little known in Scotland though the plant without the berry is sometimes seen. The berry ripens in August.

FIG. 3

The RED WHORTLEBERRY OR CRANBERRY (Scotland) (*Vaccinium vitis-idaea*), also called Clusterberry, Cowberry, Nutberry or Nuberry, Craneberry and Crawberry, a low straggling shrub with leaves resembling those of the box. The pink flowers are in terminal drooping clusters, and the berries are red. It flowers between June and August, and the berries ripen in September. Its leaves are to be distinguished from those of *Arctostaphylos uva-ursi* by the dots on the under surface and the rolled-back margins.

FIG. 4

The RED BEAR BERRY (*Arctostaphylos uva-ursi*), also called Grassack or Graashacks, a small trailing evergreen shrub which grows in dry heathy and rocky places. The leaves are finely reticulated, and the berries are red and mealy, with hard angular seeds. The rose-coloured flowers appear from June to August in terminal clusters.



C. G. M.

FIG. 1. *Vaccinium myrtillus* (Blasberry—Whortleberry—Bilberry—Whorts—Whinberry).



C. G. M.

FIG. 2. *Vaccinium oxycoccos* (Cranberry—Mossberry).



C. G. M.

FIG. 3. *Vaccinium vitis-Idaea* (Red Whortleberry—Clusterberry).
Cranberry (Scot.)



C. G. M.

FIG. 4. *Arctostaphylos uva-ursi* (Red Bear Berry—
Graashacks).



C. G. M.

FIG. 5. *Rubus chamaemorus* (Cloudberry—Averine).



C. G. M.

FIG. 6. *Empetrum nigrum* (Crowberry—Crakeberry).



C. G. M.

FIG. 7. *Erica cinerea* (Bell Heather—Fine-leaved Heath).



C. G. M.

FIG. 8. *Erica tetralix* (Cross-leaved Heath).

PLATE XXV

FIG. 1

THE CLODBERRY or AVERINE (*Rubus chamaemorus*), a small herbaceous plant belonging to the Raspberry family with large green leaves growing among the heather on the mountain tops. It has large white or rose-coloured flowers, which appear in June and July, and the bramble-like fruit is orange yellow.

FIG. 2

THE CROWBERRY (*Empetrum nigrum*), Crakeberry, Lingberry or Blackberried Heath, a small prostrate plant with the habits of a heath. The purplish flowers, which appear in May and June, are very small, and are placed in the axils of the upper leaves. The ripened berries are black.

FIG. 3

BELL HEATHER or FINE-LEAVED HEATH (*Erica cinerea*) has leaves three in a whorl. It grows on dry places and similar situations to common heather. The flower-bells are purple. The taste of the leaves is more bitter than that of common heather. It flowers in July and August, appearing before the common heather.

FIG. 4

CROSS-LEAVED HEATH (*Erica tetralix*) has leaves four in a whorl and placed crosswise. It has rose-coloured flowers, and grows in similar situations to common heather. Flowers in July and August. Grouse do not seem to care much for the two last-named heaths.

PART II.—THE INSECT FOOD OF YOUNG GROUSE BASED ON
AN EXAMINATION OF CROPS AND GIZZARDS

By Percy H. Grimshaw

The Committee have devoted special attention to the question of the food of the Grouse in the earlier stages of its existence, and have examined the crop contents of many chicks with a view to ascertaining the nature of their diet. Their dietary is extraordinarily varied, and probably we have as yet by no means exhausted the list of what they eat. It was observed from the commencement of these investigations that young Grouse were much more addicted to insect food than were the adult birds, and in order to complete the Committee's knowledge on the subject it was found advisable to obtain the services of an entomologist.

In the months of June and July 1908 the moors in Inverness-shire, Morayshire, and Banffshire and at a later period also in Yorkshire, were visited with the object of investigating the food of the young Grouse.

(1) In the first place it was desirable that a number of young Grouse chicks should be obtained, and the contents of their crops and gizzards examined, with a view of ascertaining both the nature of their food, and also, if possible, the intermediate host (supposed to be some insect or mollusc) of the Cestode parasites which infest these birds.

(2) To exactly determine the various fragments found in the crop, proventriculus, and gizzard of Grouse by the careful collecting of insects on the feeding grounds of the young birds. In many cases the remains in the crop or intestine were so broken up and crushed that it was only possible to determine and name them by careful comparison with whole specimens obtained on the same spot.¹

(3) To collect and put into spirit large numbers of insects and spiders for the purpose of dissection and microscopic examination for possible cysts of tapeworms.

The list of insects collected was most interesting, and included many rare

¹ A complete list of the insects obtained on the moors during the course of this Inquiry has been published in the "Annals of Scottish Natural History," pp. 150-162, July 1910.

species. Unfortunately, owing to broken weather, working with the net was only possible on six days, otherwise the list would have been even more representative. Most of the specimens were collected on the actual feeding grounds of the young Grouse, and the list is therefore useful as showing the variety of diet possible during the first fortnight or so of the chick's life.

On a typical Grouse moor by far the greatest variety of insect-life is found in the marshy ground around the sources of the streams. In every such place the entomologist, by using the sweeping net, finds an abundance of specimens and a fair variety of species. *Diptera* largely preponderate, but small Tineid Moths, May-flies, Stone-flies, and Spiders are also plentiful. On the higher and drier ground many other insects occur, including Crane-flies, Bees, and the larger *Lepidoptera*, as well as a few others which must be regarded as of mere casual occurrence, such as *Syrphidæ* or Hover-flies, the *Bombus* or Humble-bee, etc.

In Appendix E will be found a detailed list of the contents of the crops and gizzards of forty - five chicks examined. The birds were captured by hand and immediately killed by chloroform, dissected the same day, and their crops and gizzards transferred to methylated spirit. The contents of both crops and gizzards were afterwards examined, and the fragments carefully compared with whole pinned insects obtained on the same ground as the chicks. In many cases the remains were so crushed and fragmentary that it was impossible to ascertain their nature, beyond the fact that they were Coleopterous, Dipterous, etc. Where the generic and specific names are both given, it may be assumed that the identification is certain.

The commonest insects in the crops are undoubtedly *Diptera* of the family *Limnobiidæ*. Seventeen crops contained specimens that could be referred to this family, and of these no fewer than fourteen contained the curious little species known as *Molophilus ater*. In one case (that ticketed Moor, No. 2-22) there were over one hundred specimens of this fly. According to Dr Wilson's estimate this bird would be from eighteen to twenty days old, and its crop was gorged with the remains of *Molophilus ater*, and contained also two other *Limnobiids*, besides a few tips of heather. Other crops from the same moor, belonging to chicks a week old or less, contained fifty-six, fifty, thirty-four, and eleven examples respectively of the same fly.

Lists of
insects.

Insects
most com-
monly
eaten.

We may therefore conclude that the species is attractive to the eye and taste of the young chick. It was found plentifully in certain marshy spots where the chicks were known to feed.

Although the results have been tabulated in various ways, it has been found difficult to trace any outstanding feature regarding the insect food of Grouse chicks. With such a small number of birds it would be manifestly unwise to work out averages and curves. It is sufficient for the present purpose to show that the food of young Grouse is largely made up of insects, that these insects present a great variety of species, and that the species most commonly found in the crop is probably that which is most numerous in the area where the chicks are accustomed to feed. But it is also evident

Insect food falls off after third week. that the number of insects eaten shows a considerable falling off towards the third week of the chick's life. We should not expect the chicks to show much discrimination in the catching of their prey, and as *Diptera* undoubtedly are the most numerous in individuals of all the insects on the moors, it naturally follows that they head the list in the table of crop contents.

In the Table (p. 91) an attempt has been made to indicate, in somewhat more graphic form, the results of the examination of the crop contents. The crops are arranged, so far as possible, in order of age, beginning with the youngest. The ages of the birds are estimated by the length of the keel of the sternum or breast-bone. Relatively the ages are believed to be substantially correct, though individually there may be a discrepancy of three or four days.

The sign x in the Table indicates the presence of remains in the crop belonging to the order of insects named at the top of the column. In the third column the solid black o shows that no insect remains of any kind were found. This Table is of special importance as showing the extent to which the insect food falls off after the second week of life. This is also borne out by the great drop in the number of orders of insects represented by the crosses.

Vegetable food of chicks. The crops of young chicks in the first week or two have been found to contain, in addition to insects, the following vegetable food-stuffs in varying proportions:—

Calluna shoots; only the very fresh young green shoots are eaten.
Calluna flowers, in full bloom, and flower-buds.

THE INSECT FOOD OF YOUNG GROUSE

91

TABLE SHOWING PROPORTIONS OF ANIMAL AND VEGETABLE FOOD EATEN BY YOUNG GROUSE.

Registered No. of Bird.	Keel of Sternum in millimeters.	Insects present \pm , or absent o.	INSECT FOOD.							Age Estimate.	VEGETABLE FOOD AND GRIT.							
			Diptera.	Colleoptera.	Hymenoptera.	Neuroptera.	Arachnida.	Hemiptera.	Lepidoptera.		Heather (Calluna).	Juncus & Moss.	Bracken.	Vaccinium.	Erica.	Empetrum Nigrum.	Seeds.	Grit.
D. 10	9.75	o	1st week— 1 to 7 days old
D. 21	10.50	x	x		x	x
D. 12		x	x	x
D. 23	10.75	x	.	x		x
T. 1		o
D. 16	11.00	x	x	x
T. 2	11.25	o	x		x
D. 26		x	x	x		x
D. 15	12.00	x	x	.	x	.	x
T. 3	12.25	o		x	x	.
D. 18	13.00	x	x	.	x		x
D. 24		x	x	.	x		x
D. 13	13.25	x	x	x		x	.	.	x
D. 20		x	x	x		x	x
D. 9	13.50	x	x	7 to 18 days old
D. 5	14.50	x	x	x		x	.	.	x
D. 4		x	x	x	x	x	.	.	.		x
D. 14	15.00	x	x	x		x
D. 19		x	x	.	.	x	.	.	.		x	.	.	x	.	.	.	x
D. 2	15.25	x	x		x	x	x
D. 3		x	x	.	.	x	.	.	.		x	.	.	x
D. 7	15.50	x	x	x	x
D. 1		x	x		x	.	.	x
D. 25	15.75	x	x		x	x	.	.	x	.	.	.
T. 4		x	x	x	.	.	x	.	.		x	.	.	x	.	x	.	.
D. 17		o		x
T. 12	16.00	o	18 to 20 days old	x
D. 2	16.50	x		x
B. 3	17.25	o	x		x
T. 5		o		x	x	.	.	.	x	.	.
T. 9	20.75	o	20 to 28 days old	x	x	.	.	x	.	.	.
T. 10	22.75	x	x		x	x	x	.
T. 8		o		x	x	.	.	x	.	.	.
D. 8	24.75	x	x
T. 7		x	x	x		x	.	.	.	x	.	x	.
T. 6	26.75	x	x	x	x	x	.	.	x		x	.	.	x
B. 6	27.75	x	28 to 30 days old	x
T. 11	28.25	o		x
E. 1	30.00	x	x		x	x
B. 2	34.00	x	x	35 to 40 days old	x	.	x
B. 5	35.50	x	x		x
B. 4	36.50	x	.	.	x	6 weeks	x
B. 1	44.00	x	.	.	.	x	.	x	.	6 to 7 weeks	x	x

Moss fruit-capsules, or spore cases.

Blaeberry flower - buds, and ripe blaeberries occasionally (*Vaccinium myrtillus*).

Blaeberry leaves and young stalks.

Fern leaves (*Blechnum* and *Pteris*).

Rush heads, in flower and seed (*Juncus sq.*).

Tormentilla seed-heads.

Shoots of *Empetrum nigrum*.

Of these the most constant are the fresh young shoots of *Calluna*; then the fresh blossoms of *Calluna*, and then the spore capsules of moss. While insects are commonly eaten, many crops of the youngest chickens contained no trace of them. It is practically certain that by eating some such animal food the cystic stages of the intestinal worms which infest young birds even in the first weeks of their existence are introduced. Until this matter has been further investigated, it is needless to say more here.

PART III.—WATER

By A. S. Leslie

There are various opinions regarding the Grouse's requirements in the way of water. The majority of moor-owners and naturalists are firmly convinced that Grouse do drink, and quote in support of their view the undoubted fact that when springs and drains are periodically cleared the stock is more healthy and numerous. Others state that water is not necessary, and that the fact that drains and springs are not allowed to become choked may have beneficial results apart altogether from the maintenance of the water supply. The evidence on the subject is somewhat conflicting.

As already stated, Grouse do not appear to require water from springs or burns in the earlier stages of their life;¹ this fact is established from observations on both wild and hand-reared birds. On this subject, a well-known moor-owner in Banffshire writes: "Grouse never seem to want water except in a very dry season; a shower is sufficient to last them for a long time. The less water they have in hand rearing, I find, the better they do." And, again, "I have never noticed that the young Grouse, when half-grown or older,

¹ *Vide* chap. ii. p. 18.

require more water than what they pick up in the grass in wet weather, and what is sprinkled on the grass or heather at meal times in dry weather. Old Grouse seem to know how much is good for them; while young Grouse, if allowed access to water, are almost certain to drink too much, and scour. This, of course, refers to tame birds." Another correspondent of the Committee, a gamekeeper near Pitlochry in Perthshire, writes: "Regarding water, I have known several broods fetched out 600 yards from the nearest water of any kind, in a dry season, and they continued to thrive without water for at least three weeks after hatching, when rain would no doubt relieve the old bird, which I am of opinion had nothing to drink but dew all that time; at least I never found young chicks without the parent bird along with them."

On the other hand, a gentleman in Yorkshire, who successfully reared twenty-four Grouse out of twenty-eight eggs set, says: "They were watered three times a day." And a gamekeeper, whose experience of some of the largest moors in Perthshire has lasted for a lifetime, says: "There must be water, and, where a moor is blest with good springs, there will the Grouse be also. One cannot have too many springs on a moor in dry weather."

When full-grown there is little doubt that Grouse do drink; hand-reared birds are seen to drink frequently on a hot day from the supply of fresh water provided for them, and the droppings of nesting birds are always found near water. Wild birds, in the hot weather of July and August, and in the dry, frosty days of winter, often congregate near running water and open streams when other drinking-places are dried up or frozen hard. It is well known that in the summer Grouse often shift entirely from the drier beats of a moor to the well-watered ones, and, on a certain dry, sandy moor near the sea, the young birds die if the artificial drinking-pools are allowed to run dry. The almost unanimous opinion expressed by correspondents favours the view that under natural conditions the adult Grouse go to drink two or three times a day.

In support of the view that Grouse either never drink, or at least are not dependent upon a supply of drinking water, several arguments are brought forward. It is said that no Grouse has ever been seen to drink, but when we consider how wild the bird is in its natural state this is not surprising; indeed, only very few observers have succeeded in seeing the bird in the act of feeding. Another argument used is that from an examination of the alimentary canal no trace of water can be found, and the contents

Evidence
in favour
of Grouse
drinking.

Arguments
that
Grouse do
not drink.

of the crop are always found to be dry. This may be sufficient to prove that the bird does not drink when the crop is full, but does not dispose of the possibility of its drinking during the long periods of the day when the crop is empty. Then, again, cases are quoted of moors which carry a large and flourishing stock of Grouse where the ground is by no means well watered. On one of the best stocked Grouse moors in Britain, the only water comes from about a dozen springs and one deep burn which runs through the middle of the ground. Grouse are seldom observed to resort to the burn, and it is difficult to see how several thousand birds can all water at the springs. While it cannot be said that this entirely disposes of the water drinking theory, it seems to justify the view that Grouse are not dependent upon a large water supply.

How far dew forms a substitute for water is a matter which the Committee consider of great importance, and one to which they have given considerable attention without arriving at any results sufficiently definite to be worth reporting. There is a curious lack of information available regarding the fall of dew, the districts in which dew is most prevalent, etc. There is probably a close connection between dew and the infection of Grouse by the nematode worm *Trichostrongylus pergracilis*. In view of the fact that the larvæ of this worm can only climb the heather shoots, or indeed exist on them, when they are slightly damp, the Committee believe that this is one of the questions which might be further investigated with advantage.¹

PART IV.—GRIT

By Dr H. Hammond Smith and R. H. Rastall

The health of Grouse and of other game-birds is greatly dependent on the nature of the grit they take to assist in the assimilation of their food.

Necessity of grit. During the autumn of 1906 the Committee made a collection of the grits from the gizzards of Grouse and other game-birds. This collection formed the subject of a paper read by Dr Hammond Smith at a meeting of the Zoological Society in May 1907. These grits were obtained from the gizzards of Ptarmigan from Ben Mohr in Sutherlandshire; Grouse from Ross-shire, Inverness-shire, Aberdeenshire, and

Collection made by Committee.

¹ *Vide* chap. x. pp. 228, 233.

North Wales; Blackgame from Ross-shire and Exmoor; and Partridges and Pheasants from various counties in England and Scotland.

The gizzards of Grouse naturally received most attention; but for purposes of comparison those of other game-birds were also examined. The quantity of grit found in a single gizzard varies very slightly. Samples taken from adult cocks were each found to be equal in bulk to an ounce of shot, although, of course, much lighter, and the number of grains in each ranged from three hundred and fifty to five hundred and fifty. It was also noticed that, especially in the case of Pheasants, the cock birds have a larger quantity of gritty material, while the individual grains also appear to be larger. This is doubtless correlated with the larger size of the bird, for in the smaller varieties of game-birds and in immature individuals it is invariably found that the grains of grit are fewer and smaller than in the larger and full-grown specimens. The gizzard of a chick of fourteen to twenty days old was examined, and the grit was found to weigh 3 grains. It consisted of fragments of quartz, smooth and water-worn, and evidently picked up in the bed of a stream. *Two* only were minute but perfect prisms of quartz, quite unworn. All the grains were decidedly smaller than in an adult. In a half-grown chick the grit weighed 58 grains, while in adults the average weight is 118 to 120 grains. Grits are present even in very young birds; in one case they were found in a chick only forty-eight hours old.

Bulk of
grit found
in each
gizzard.

Size of grit
particles.

Weight of
grits.

The grit of an old bird can be at once recognised by the large size of the grains, and by the excessive polish and smoothness of the well-worn surfaces, suggesting that the larger grains are in use for a considerable period of time. Between extreme youth and old age all stages of wear and polish may be found as well as every gradation in point of size.

A full analysis of the petrological character of the specimens is contained in the Interim Report of the Committee; it is unnecessary to repeat all the details here, but a short summary of the general conclusions may be given. As would naturally be expected the constituents of these samples are nearly always hard rocks and minerals. Minerals or rocks softer than quartz, flint, or felspar are hardly ever found; this may be due partly to selection by the bird, but it must also be borne in mind that soft substances would soon be ground up by the action of the gizzard, and disappear. To this also is probably due the almost complete absence of any calcareous matter,

Constitu-
ents of grit.

which is both soft and comparatively soluble. The only really abundant constituents in the gizzards of Grouse are quartz and felspar, and small fragments of various rocks composed of one or both of these minerals, such as granite, gneiss, quartzite, etc., with occasionally grains of shot and crystals of garnet, and other minerals. Felspar is chiefly found in specimens from Scotland and North Wales, where rocks consisting largely of this mineral are specially abundant. The specimens from Ross-shire are of interest from the geological point of view, since in some cases they contain a representative collection of the gneissose and schistose rocks of the north-west Highlands.

A comparison of results shows that in the gizzards of Grouse quartz is nearly always present, although no quartz may be found on the moor where the bird was shot. Two cases of this may be mentioned. On one part of an extensive shooting in North Wales there is excellent feeding and sheltering ground for Grouse, but no quartz grit, yet the gizzards of the birds always contain

quartz; in order to obtain it they have to fly across a wide valley to another hill, and then return again to their feeding-ground.

Again, on a Ross-shire moor no quartz could be seen on the moor, yet all the gizzards of these birds contained quartz; it was found that

this quartz was probably obtained from the burns, for on examining them small pockets of water-worn quartz were found in many of the pools and eddies.

The quartz is not always angular and sharp, but is frequently water-worn; in these cases it is probably picked up out of burns — in fact, in low-lying moors the water-courses are almost sure to be the source of this quartz.

The grits found in the gizzards of Yorkshire Grouse are very similar to those of the Scotch birds except in one case, where the grit is chiefly composed of small black pebbles. In one gizzard out of every three of the Grouse examined shot were found; but shot were rarely found in the gizzards of Pheasants.

The mineral contents of the gizzards are very fairly representative of the harder rocks and minerals of the district from which each is derived,

but it may be noted that whereas Ptarmigan and Grouse seem unable to exist without quartz, Partridges, and still more Pheasants, are more adaptable; they prefer quartz if they can get it, but failing quartz, Pheasants will content themselves with flint, sandstone, and even coal. Doubtless the tough and fibrous nature of the food eaten by Grouse

Quartz
present in
gizzards
though not
found on
moor.

Partridges
and
Pheasants.

makes it necessary for him to confine himself to the hardest and most angular descriptions of rock, and even when quartz grits are found in the gizzard the angles are often rounded and smooth from the nature of the work which they have been called on to perform. Flint grit may serve for Pheasants, but it does not fracture into serviceable shapes for Grouse. Sharp points and cutting edges are not wanted, but sub-angular and roughly rounded pebbles of small size for the breaking up and pulping of the comparatively hard foliage of *Calluna*.

In another part of this Report it is suggested that when quartz is scarce it might be artificially introduced with a view to the welfare of the stock. This expedient has met with some success, but has not been very extensively adopted. The artificial introduction of quartz grit has frequently been tried with Pheasants, and always with success. In the Committee's collection there are several specimens of gizzards from Pheasants shot on estates both before and after the introduction of quartz, and in every instance it can be seen that the quartz is preferred to the natural grit found on the estate.

Observations have been made with a view to finding out how long quartz or other hard grits normally remain in the gizzard of a Grouse, and it has now been proved by experiment that if none are supplied to make good the normal and presumably accidental loss, the bird whose gizzard may on the first day have allowed about a hundred grits to pass, becomes exceedingly careful on the second and third day, and allows no such loss to occur again. In a case in which no grits were supplied to a Grouse at all, and in which the grits passed in the droppings were carefully washed out and collected every day for twenty-one days, the greatest daily loss after the second day never exceeded thirteen small pieces, even though a hundred and sixty pieces had been passed on the first day, and twenty-seven pieces on the second. This bird died unexpectedly on the twenty-first day, and upon dissection the gizzard was found to contain still no less than half of the original contents, all of which had been in the gizzard for at least three weeks. That this apparent control of the gizzard over the loss of grits was not merely accidental was proved by the occurrence of a precisely similar series of losses day by day in another bird; but when its companion died, apparently as the result of losing half its grits, the second bird was not pressed to a similar finish.¹

It is therefore probable that in the ordinary course of a Grouse's life the

¹ For detailed description of experiments in Grit Starvation, see vol. ii. Appendix F., part (1).

daily loss of small grits is considerable, and that this loss is replaced by an equally regular supply picked up day by day upon the sides of moor roads, or in "scrapes," or along the channel of a burn.

But, in the event of a heavy snowfall it appears very probable that the Grouse soon recognise that the loss is exceeding the amount which can be made good day by day, and that in such a case they can, in some unexplained way, place a check upon further loss. It cannot for a moment be imagined that the bird has any sort of voluntary control over the passage of grits from the gizzard. But it is quite conceivable that the gizzard itself will allow a certain careless loss of any surplus number, especially of the smaller pieces, so long as there is still a sufficiency of larger grits in the gizzard.

When the supply, however, is straitened, and the bird fails to find more grits to swallow, it may be that less food is eaten as well, and thus the loss of grits is automatically reduced. This is probably the explanation which comes nearest to the truth, and it is a significant fact that a bird not only loses weight, but may actually die when only half of its normal supply of gizzard grits has been lost, and when the dejecta show that this amount of grit is still capable of grinding up the food given to it.

Under normal conditions the character of the grit required differs with the nature of the food that is being eaten. With hard grain or seed, or with berries containing seeds, it is badly needed, and must be obtained if the food is to be digested. Oats and oat husks are all efficiently dealt with by the quartz grit normally found in a Grouse's gizzard, but large hard seeds are not, and are passed undigested. These seeds, however, are sufficient in themselves to pulp fruits so long as fruits only are being eaten. But as soon as heather or other fibrous vegetable matter is eaten, quartz or other stone grit becomes essential.

The possibility has been suggested that the replacement of quartz grits by hard seeds of fruit, and the passage of the former through the intestine may act as a vermifuge. So often has a diet of berries apparently arrested a case of Helminthiasis that it is a question to be seriously considered whether enough attention is given to the encouragement of berry-bearing plants upon a moor. In many cases the sheep keep them so closely cropped that except where there are woods or enclosures it is difficult to find a visible trace of them. It would perhaps repay the trouble

Control
useful in
time of
snow.

Berry seeds
as a vermi-
fuge.

and expense to fence off enclosures from the sheep where any tendency is seen for the growth of Blaeberrries, Cranberries, Crowberries, or the like, and the Grouse would quickly find and make use of them.

No. 1215 may be cited here as a case in point, for the bird was an obviously convalescent hen Grouse of 16 ounces, with every sign of excessive Helminthiasis, but a complete absence of *Davainea*, and only one or two portions of *Hymenolepis*. *Trichostrongylus* alone was present in great numbers. The gizzard contained no quartz, but was full of hard seeds (clusterberry or *Vaccinium Vitis-idaea*). The small intestine, full of food, was very irregularly contracted, and contained not only many unbroken clusterberry seeds, but quartz grits as well, while the rectum contained the same, and exhibited a considerable amount of punctiform, villous reddening, especially in the lower third.

Grouse No. 1228 was a rather similar case, the gizzard being crammed with hawthorn seeds, and having no quartz at all, while the small intestine was very much irritated, had its vessels all fully injected with very fluid contents, and yet no *Davainea* at all. The rectum was again red with injected villi. This bird was caught sick. It was a case of Strongylosis in a hen of 13 ounces only.

In the Blackcock the gizzard with its quartz pebbles can crush hawthorn pips, but the Grouse apparently cannot crush any of the pips or even much smaller berries such as Clusterberry, Blaeberry, or Crowberry. They all pass through intact. Nos. 1265, 1723, 1733, 1735, 1817 are all cases in point.

It is particularly unfortunate that during deep snow, when Grouse have great difficulty in replenishing their stock of gizzard grits, they are compelled by hunger to feed upon the very foods which most rapidly evacuate their entire stock of grits. The hips and haws whose large hard seeds, as has been said, quickly replace the quartz in their gizzards, are comparatively useless to them for dealing with heather or Blaeberry shoots, yet the bush and tree fruits are amongst the first emergency rations used in a heavy fall of snow, since they come within reach as the ground foods become more deeply buried.

The strongest evidence that quartz is the most suitable form of grit is its universal presence in all the vegetable feeding birds that can obtain it. Red Grouse, Ptarmigan, Blackgame, and Capercailzie, as well as Pheasants and Partridges bred on the moor borders, and Scandinavian Willow Grouse, all collect quartz, and nothing but quartz, if it is by any means to be obtained.

CHAPTER V

PHYSIOLOGY AND ANATOMY OF THE RED GROUSE

By Edward A. Wilson

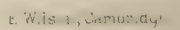
As a preliminary to the proper understanding of the method of infection in the forms of "Grouse Disease" known respectively as Strongylosis and Coccidiosis certain facts concerning the functional activities of the different parts of the Grouse's alimentary canal should be explained.

By the alimentary canal is meant the whole tract of the digestive apparatus from the mouth, to the anus or vent; and the following is briefly a history of the experiences undergone by a morsel of food after it has been swallowed by a healthy bird.

In the case of the Grouse it is reasonable to take a small sprig of heather, *Calluna vulgaris*, with a somewhat woody stalk and a number of very small greenish or brownish green leaves, and perhaps a few small pink flowers or shrivelled flower heads containing a considerable number of very small seeds. Other foods of course are frequently eaten, but all the vegetable stuffs may be considered as partly composed of soft, alterable, and digestible material, such as starch, protoplasm, chlorophyll, and sap solutions, and partly of indigestible woody fibres. The animal foods, whether they consist of insect or mollusc, worm, crustacean or spider, can also be considered as composed partly of soft, digestible material, and partly of indigestible matter, such as chitin.

And further, the function of the grit must be considered, since it is as essential to the well-being of a herbivorous or graminivorous bird as are teeth to the higher mammals.

The sprig of heather is partly plucked, partly cut from the growing plant by the beak of the bird. In captivity it is found necessary to fix the bunches of heather either by tying them to the wire run or by placing a heavy weight upon



the roots; should this precaution be neglected the bird, having no notion whatever of using its feet to steady anything, drags the loose heather all over the ground in unsuccessful efforts to pluck off the tips.

There is sometimes to be seen quite a free flow of watery saliva from the beak of a feeding bird, and in the mouth of birds killed there is always a certain amount of saliva. This saliva serves to coat the rough hairy heather tip with mucus, and thus to facilitate its passage down the *oesophagus* ^{Saliva.} to the crop (Pls. XXVII.a, XLIV.). The food is, of course, swallowed whole but in very small pieces, and there is no mastication. The length of the *oesophagus* (Pls. XXVI. œ., XXVII., Fig. 1 (a), XLIV.) from the pharynx to the proventriculus is $5\frac{1}{2}$ inches (=140 mm.), when the neck is normally outstretched; but before passing down the whole length of this tube the food finds ^{its way} *oesophagus* into a thin-walled sac or diverticulum of the *oesophagus*, at a point 3 inches, or 75 mm., from its entrance at the pharynx, and commonly called the "crop" (Pls. XXVII.a, XLIV.). Here the food collects, and ^{Crop.} remains for a longer or a shorter period according to the rate at which the gizzard can dispose of it. The latter portion of the *oesophagus* measures 2 inches (=50 mm.) in length, and the opening of the crop occupies about 17 mm. of the front wall of the *oesophagus*. The proventriculus (Pls. XXVI. Pr., XXVII., Fig. 1 (b), XLIV.) forming the thick-walled ^{Proven-} *tricus.* glandular part of the stomach has a cavity of very small dimensions, and a length of $\frac{3}{4}$ inch (=20 mm.). It is lined with large mucous glands having prominent mouths. These secrete a thick, tenacious, opaque white fluid, wherewith the morsels of food on their passage from the crop to the gizzard are coated.

In this respect there is a very great difference between the condition of the food as it leaves the crop, and its condition in the actual gizzard. In the crop the food is almost invariably dry, almost exactly as it is plucked from the living plant, and it is found thus in masses fresh and green, or greenish brown, with no appreciable admixture either of mucus or of water.

This almost universal dryness of the heather, or other Grouse food, as it is found in the crop, militates strongly against the idea which is occasionally suggested that the Grouse is a thirsty bird by nature, and must have an abundant supply of water. This is almost certainly ^{Food in crop normally dry.} not the case, for the very rare instances in which the contents of the crop

were found distinctly wet, were, without exception, in birds showing definite signs of sickness, and in sickness there is no doubt that the bird seeks water and often drinks it. It is, however, very possible that water is swallowed straight into the proventriculus, passing by without entering the opening into the crop. If this be so, too much stress must not be laid on the dryness of the food in the crop, in considering the drinking habits of the bird.

But with food in the crop, and there is no hour in the day when the crop may not contain some food, all the evidence afforded by an examination of many hundreds of crop-contents goes to prove that water is not freely taken, or if taken, is not admitted to the crop. Probably, when there is food in the crop, no water is drunk, for there is no general condition of wetness at any time either in the crop or in the proventriculus, or in the gizzard, all of which are occupied in turn by the gradual passage downwards of the morsels of food collected in the crop.

In the proventriculus, as has been said, the bits of food, coated now with a tenacious and slightly acid mucus, are passed into the muscular gizzard (Pls. XXVI. (G.), XXVII., Fig. 1 (c), XXVII.a, XLIV.), a familiar object in the anatomy of the common fowl, and an organ of very similar shape and of equal muscularity in the Grouse. Its walls are very thick, and the muscles which compose them act from tendinous sheets, into which they are firmly fixed. The cavity of the gizzard is comparatively small, and is lined with a very tough resistant lining membrane of fibrous tissue, and contains about a teaspoonful of small hard subangular or rounded grains of hard rock.

The substance almost universally chosen by the Red Grouse is quartz, and although on the moor, as in captivity, the bird will swallow any small portion of hard material which comes in its way, quartz is most suitable, not only for the Grouse but for every other graminivorous bird in health. A very extensive collection of Grouse's gizzard grits has been made by the Committee, and carefully examined, and the result shows the variety of material of which a Grouse will make use when quartz is not locally abundant.¹ But the point conclusively proved is that quartz, both on account of its hardness and its method of fracture, is the gizzard grit most abundantly used by Grouse. The subject of gizzard grit is more fully dealt with in chapter iv.

¹ *Vide* chap. iv. p. 95.

PLATE XXVII.

Fig. 1.

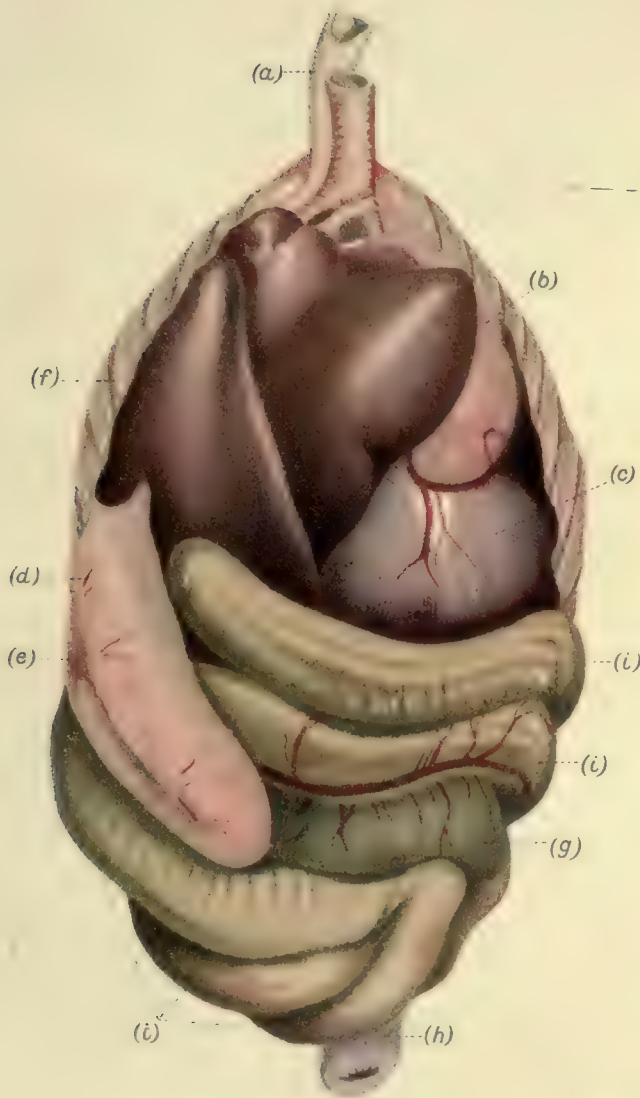


Fig. 4.

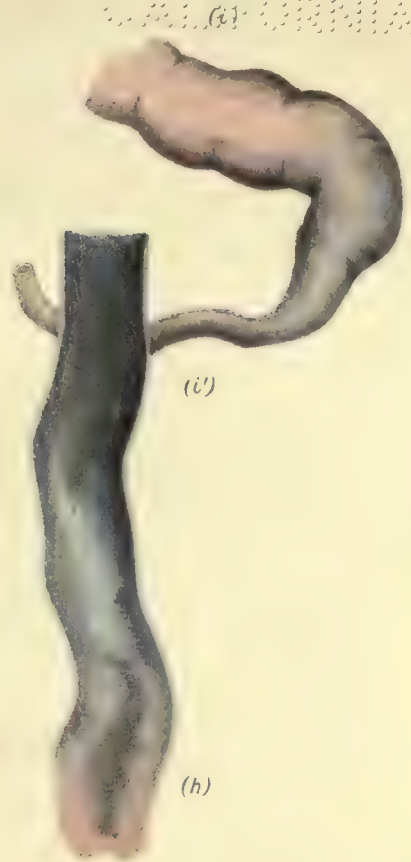


Fig. 2.

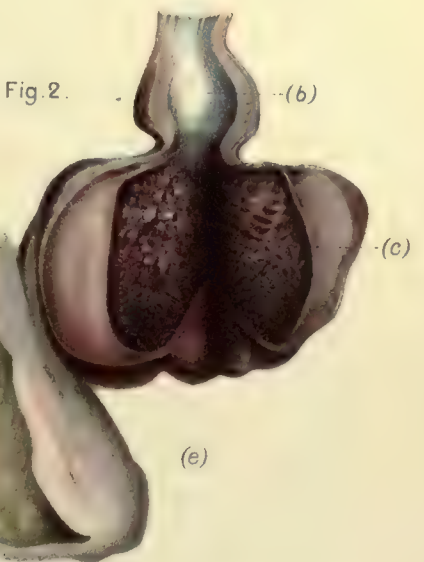
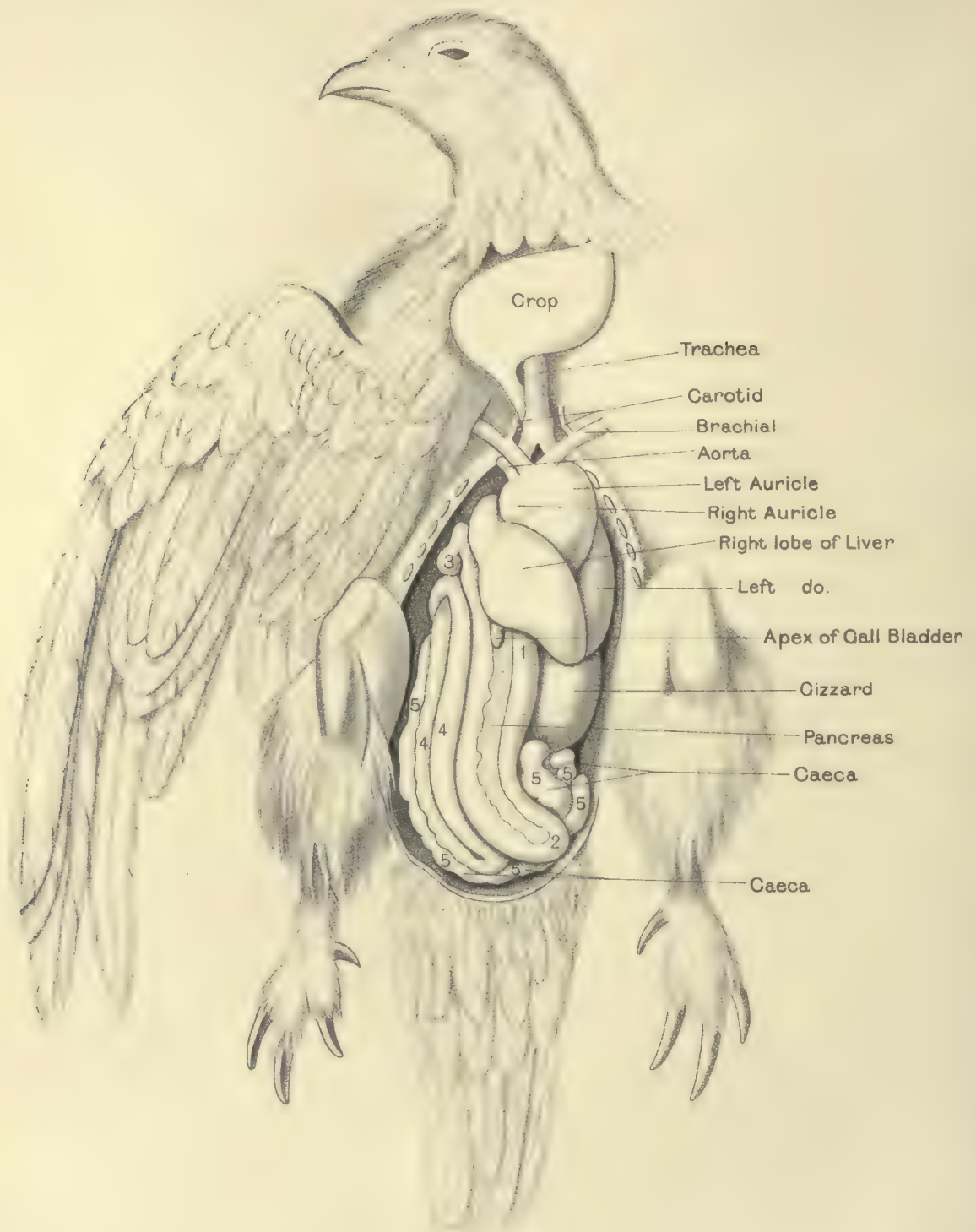


Fig. 3.



PLATE XXVIII.



E. Wilson, del. et. lith. Montagu.

Lead pellets are often picked up by the bird amongst other objects, and swallowed because they are hard and small; but the suggestion that lead poisoning has ever resulted either in this or in any other way from the scattering of leaden shot over a moor must not be taken too seriously.

Lead pellets in gizzard.

The food then having reached the gizzard with a free admixture of slightly acid mucus, is now thoroughly mixed up with the grits of quartz, and ground with their assistance to a pulp, the harder woody fibres soon showing up as whitish bits in a brownish, greenish, or reddish mess. This vegetable pottage has now to be separated from the quartz grits, and to be passed little by little into the duodenum.

Action of gizzard.

The separation is effected at the distal sphincter muscle of the gizzard, and it often appears as though the sphincter was unable to distinguish readily between the feel of a quartz grit and the feel of a hard seed, or the woody "stone" of a berry. It is by no means rare to find, when a bird has been feeding for a time on berries or wild fruits, that the gizzard loses all its rock grits, and contains nothing harder than seeds, pips, or woody "stones." Concurrently with this, it is sometimes found in birds which, from their condition, one would have expected to have contained tapeworms in abundance, that the intestines below are entirely clear of these parasites. We are thus tempted to think that the passage of a number of quartz grits and hard seeds may have so stimulated the peristaltic action of the intestine, and at the same time have so damaged the tapeworms that the latter have been broken off at the neck and discharged *en masse*. The worms may grow again from the attached head or scolex, but it is possible that even the scolex may in many cases be dislodged, and for that reason the advisability of encouraging such Grouse foods as have big seeds and hard berries has sometimes been advocated.

Separation of food from grits.

Effect of grits passing into intestine.

Be this, however, as it may, the digestible food, including our particle of heather, now sufficiently pulped in the gizzard, is separated as it leaves the gizzard from most of the harder and larger grits, and enters the duodenal loop of the small intestine.

The duodenum (Pls. xxvi. (D.), xxvii., Fig. 1 (*d*), xxvii.a, 1-2, XLIV., 6 $\frac{3}{4}$ inches (=170 mm.) in length, begins at the exit of the gizzard and is U-shaped. It consists of two parallel "limbs" of about equal length. These two limbs are supported and held together by a mesentery

Duodenum.

which contains the pancreas (Pls. xxvi. Pa., xxvii., Fig. 1 (e), xxvii.a, xxviii., Fig. 1 (e), XLIV.), a pale pink, flattened glandular mass filling the space between the descending and ascending limbs. This gland pours its alkaline and digestive pancreatic juice and ferment into the upper end of the descending loop.

The liver (Pls. xxvi. (L.), xxvii., Fig. 1 (f), xxvii.a), also pours its alkaline, biliary secretion into the upper end of the descending loop, so that it is intimately mixed with the pulped food as it passes into the duodenum little by little. The shape of the loop assists this admixture, since it checks the immediate passage of the contents into the convolutions of the upper small intestine.

Digestion is now ready to go on apace. The food, when being macerated and pulped in the gizzard, is distinctly acid; but, when mixed with the alkaline pancreatic and hepatic secretions from the liver, becomes gradually neutralised until it is of the right reaction as well as at the right temperature for the action of the digestive ferments.¹

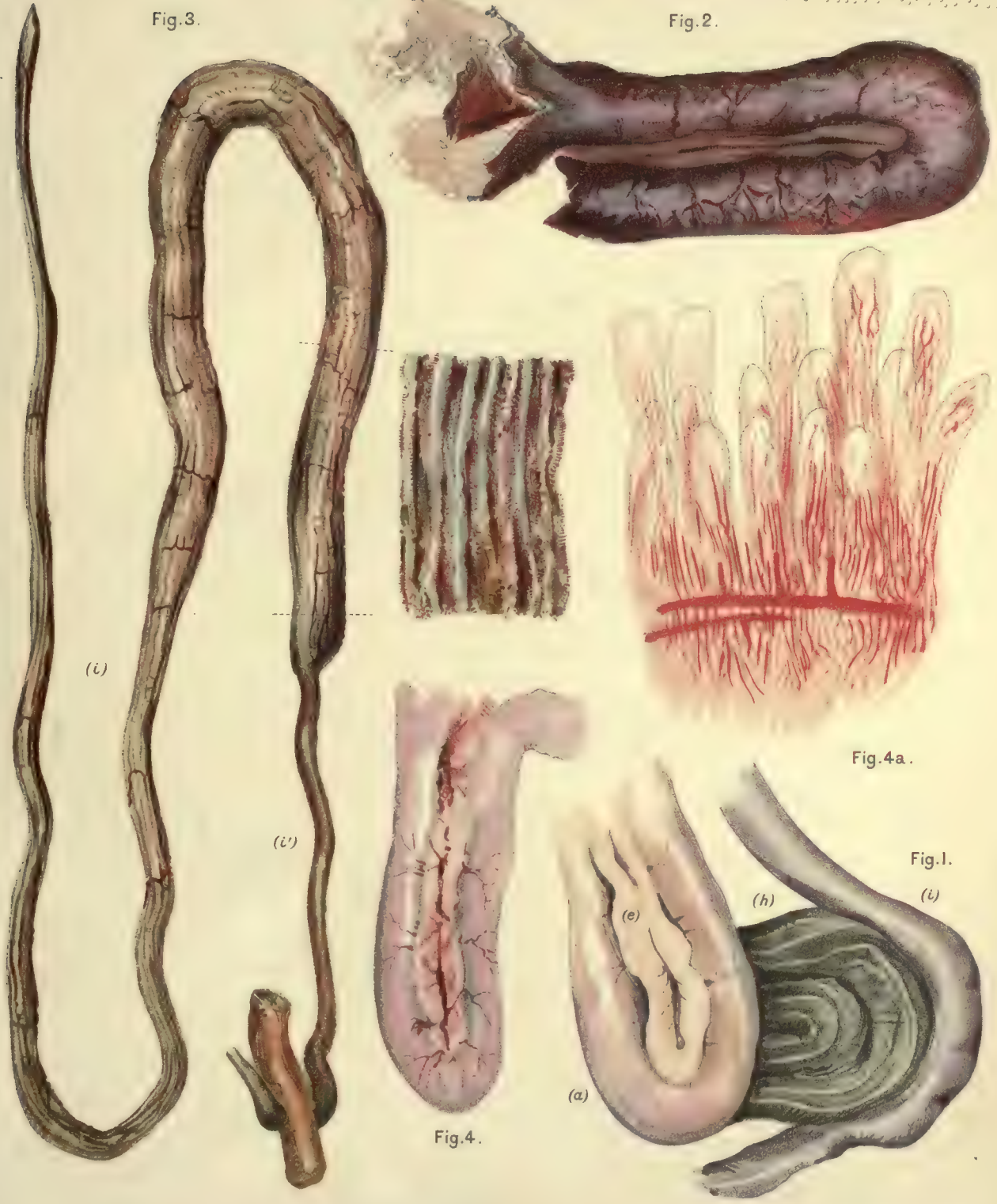
In the duodenum the contents are normally almost fluid, when there are no tapeworms or threadworms present. The duodenum is, however, the common habitat of *Hymenolepis microps*, and of *Trichosoma longicollis*; and the former of these is frequently present in such large numbers as to appear like a soft, semi-solid, creamy mass completely filling the whole length of the duodenum (Pl. xxviii., Fig. 2).

It is only when this worm is absent, as it generally is during the winter months, that one appreciates the fact that the duodenum seldom contains at any one particular moment more than a very small amount of solid food pulp mixed with the digestive fluids. The passage of the food through it is very gradual, and the admixture with the alkaline digestive juices is proportionately complete.

Normally the outward appearance of this part of the intestine is a pale creamy white, and the mesenteric vessels which ramify over the peritoneal surface are almost invisible. The pancreas also should be pale creamy white or faintly pink (Pl. xxviii., Fig. 1 (a) (e)).

The alkaline mixture now passes from the duodenum into the convoluted upper portion of the small intestine (Pls. xxvi. (C.S.I.), xxvii., xxvii.a, XLIV., Fig. 1 (g)). This extends from the lower end of the duodenum to the upper end of the rectum (Pls. xxvi. (R.), xxvii., Fig. 1 (h) XLIV.),

¹ *Vide* pp. 105, 106.



E. Wilson, Jambrid. pr.

where the two cæca enter it. The small intestine measures in all 35 inches (=872 mm.); but there is a distinction to be made between the upper or proximal convoluted portion which is attached to a wider mesentery, and the lower or distal straighter portion (Pl. xxvi. s.s.i.) which is attached to a much narrower mesentery. And, while there is probably a difference in the character of the glands which form the mucosa of these two portions, the chief obvious distinction is that the convoluted portion is freely moveable, whereas the straight portion is so intimately folded with the long cæcal appendices, and so closely bound together with them in a common mesentery as to be very limited in its movement. The various parts of the lower intestine are shown laid out in the accompanying diagram (Pl. xxvi.), while the next diagrams shows them as they appear in their normal condition in the body cavity of the bird (Pl. xxvii., Fig. 1, xxvii.a).

Returning, however, to the changes which are being experienced by the particle of food in question as it passes from the duodenum into the convoluted portion of the main gut, it is first noticed that the accompanying duodenal tapeworm, *Hymenolepis microps*, wholly disappears, and that its place is taken by the much larger and more conspicuous tapeworm, *Davainea* ^{Large} *urogalli*, often in such quantity that the outward appearance of the ^{tapeworm.} small intestine is altered to a swollen, bulky gut of a creamy white colour due to the enclosed mass of tapeworms shining through the thin and distended walls.

Another point has already been noticed, namely, that the neutral or faintly acid reaction of the contents of the duodenum now gradually changes to a more and more markedly alkaline reaction. *Hymenolepis* affects a neutral medium, and *Davainea* an alkaline medium.

These changes in the character of the intestinal contents can, of course, be easily tested by the use of litmus papers; but when a Grouse, which has been feeding upon ripe Blaeberrries, Cranberries, or Crowberries with coloured juices, is examined, the contents of the alimentary canal of the bird itself are found to be coloured within from end to end, in such a way as to make litmus unnecessary. The juices of the berries are red, and stain the tissues red wherever the acidity is not overcome by alkaline digestive juices. But wherever there is a slight alkalinity in the juices there the tissues are stained bluish. This is shown in the accompanying figures, which are drawn directly from the dissection of a berry-feeding Grouse (see Pl. xxvii., Figs. 2, 3, and 4).

Fig. 2 shows the food contents to be blue while in the proventriculus (alkaline), on reaching the gizzard (acid) they change to reddish purple, in the duodenum (slightly acid to neutral) they lose much of the red tint, but it is not until they enter the small intestine (alkaline) that they again resume the blue colour (*see* Fig. 3, representing one of the coiled loops of the small intestine), the alkaline reaction continues throughout the length of the small intestine as far as the lower end of the rectum (Fig. 4 (*h*)), where it becomes slightly more acid, and the acid reaction of the cæca (Fig. 4 (*i*)) also causes the colour to change to a reddish tone.

In the convoluted intestine the food is in a somewhat fluid state ; and as the mere presence of convolutions in the intestine of any animal are evidence of the necessity for a retarded passage, the function of the convolutions in this case is obviously to hold the mixture for a sufficient length of time at a certain regular temperature in order to give the active digestive ferments every chance of completing their work upon the food-pulp. The heather-pulp is thus altered, so far as its alterable part is concerned, into a solution of assimilable food and an indigestible refuse of woody fibre. The raw material here becomes the digested material ready for use by the tissues of the body as soon as it can be brought to them by the agency of the circulating lymph and blood. Certain harmful and poisonous products will also unavoidably appear in the Grouse's intestine as they do in the human intestine and in the intestine of every living animal from time to time, even in the ordinary course of digestion. These, as in the human body, having been absorbed with the soluble food supply into the blood are then eliminated, chiefly in their passage through the liver, before the mixture of good and evil products can be thrown upon the general circulation. The liver in man is the great eliminator of poisons produced in the intestine, and the liver in the Grouse almost certainly acts in a similar way.

There is probably some selection and some chemical alteration during the passage of the food, including that part of our heather fragment which has now been digested, through the mucous membrane into the blood-vessels.

By the time the food reaches the lower and straighter portion of the small intestine it is seen that much of the fluid has disappeared, the contents are becoming more and more thickened, and are now converted into a semi-fluid paste interspersed with woody particles. By the time that the contents reach the junction of the small intestine with the rectum they have been still further

prepared for separation. At this point the cæcal appendices (Pls. xxvi. c1, c2, xxviii., Fig. 3 (*i*), xlv.) open into the main gut, and all that is soft is now squeezed into the narrow openings of the cæcal appendices; ^{Cæca.} while all that is hard, including the indigestible part of the heather fragment, the indigestible woody fibres, and the refuse of the cellular tissues, is compressed into a firm, dry mass, and so passed straight into and along the rectum.

Each cæcal appendix measures from 30 to 36 inches (762 to 915 mm.) in length. Their colour in health is a dull drab grey, while that of the small intestine is greenish; the difference in colour between portions of the alimentary canal are shown on Pl. xxvii., Fig. 1, representing the normal duodenum (*d*), pancreas (*e*), small intestine (*g*), cæcum (*i*).

When excrement leaves the body of a normal healthy Grouse it does so in two distinct forms. The firmer excrement described above passing through the rectum leaves the body first, and either immediately, or after a short interval, the more fluid and pasty unabsorbed contents of the ^{Two forms of excrement.} cæcal appendices follow without having mixed at all with the dejecta of the main gut.

The dry and often quite hard Grouse "dropping," which outlasts much weathering, can be seen on many moors without any particular search, sometimes at every yard or two upon bare burned ground, where it becomes bleached almost white under the combined action of sun and wind before it is broken up to be disseminated as dust.

The matter is one of some importance, for the perfectly normal cæcal dejecta of the Grouse are so often considered abnormal, and even pathological, by gamekeepers and by sportsmen, and are so constantly credited with having some mystic relation to "Grouse Disease" that it becomes necessary to explain the appearances in detail.

In walking over a well-stocked moor, in fairly dry weather, Grouse's droppings are to be seen lying in small heaps upon the ground where birds have "jugged" or roosted amongst the heather at night. It is sometimes surprising to see how many of these compacted rolls of undigested woody fibre are passed by a single bird in one night.

Each hour throughout the roost there appears to be a separate motion, and always of the hard "formed" dropping coming directly from the main gut, and not of the pultaceous, soft, cæcal matter. But, when morning comes, and especially when the bird has moved to the neighbourhood of water for the

purpose of drinking, the cæca discharge themselves, and the typical soft cæcal dropping, which is so frequently misinterpreted as a sign of sickness, is then deposited either upon the harder dropping of the night if the bird has not already moved away, or more usually somewhere in the near neighbourhood.

During the night the main gut and the cæca appear to be engaged in a divided labour. While each cæcal appendix is employed in the absorption of nutritious, fluid solutions from the soft mass of food within it, the lower part of the small intestine is continually receiving from above more and more of the mixture of soft digested pulp and hard indigestible waste matter.

The exact method of separation is due to the action of the sphincter muscles which regulate the opening and closing, not only of the two entrances
Method of separation. to the cæcal appendices, but also of the entrance to the upper end of the rectum.

There are no actual valves and no visible folds, but each cæcum at its junction with the main gut is guarded by a narrow tubular portion (Pls. xxvi. c1, c2, xxvii., Fig. 4 (*i*), xxviii., Fig. 3 (*i*)) some 4 or 5 inches (102 or 127 mm.) in length, which is lined by a mucosa rich in small projecting papillæ, and which admits nothing to the cæcum except the softer parts of the pulpy mixture. The pultaceous, creamy-brown pulp must be thus squeezed into these cæcal back-waters by the peristaltic pressure of the small intestine from above, while the rectum at the same moment refuses to admit anything at all.

Each cæcum has one blind end and one end opening into the upper part of the rectum. All the useful contents of the main gut must pass into the cæcum, and the undigested portion must pass out again by the same orifice. Yet the cæca always appear to be filled to some extent by material from one end to the other. It is only after a prolonged starvation, say for twenty-four hours or more on a railway journey, that the cæcum is found in the condition represented in Pl. xxviii., Fig. 3 (*i*), and it is obvious from this figure that the
Manner in which cæca are emptied. riddance begins by contraction of the blind end, and that it gradually works toward the open end. It would appear from this that there must be a pause in the entrance of material to the cæca while they are evacuating the waste matter. The musculature of the small intestine seems thus to act intermittently but frequently, and without any long period of rest. The cæcal musculature, on the other hand, must have long periods of rest when the cæcum is full or actively absorbing, and then a period of activity to empty itself. But these periods of rest and activity must be of very different length. It is con-

ceivable that after full feeding in the evening the Grouse jugs in the heather, and the process of digestion and the action of the intestine proceed until there is a large quantity of hard and soft food in the lower part of the small intestine ready for selective absorption and separation. This separation probably proceeds all night, the soft material constantly passing *into* the cæca, and the harder waste matter passing on as constantly into the rectum and out at the vent.

Then, early in the morning the action is reversed, the passage of food down the main gut ceases because the supply from above has been stopped during the night when, of course, nothing has been eaten. The useful part of the cæcal contents has now been absorbed, and is circulating in the blood, and the cæcum therefore contracts downward and expels all the waste matter that is in it. This is borne out by what one sees upon the moor, by the absence of cæcal excreta amongst the heap of formed droppings passed in the night, and by the occasional appearance of some cæcal excreta on the top of these heaps, though more frequently in their near neighbourhood or near the early morning drinking and feeding resorts. There is, moreover, now no doubt that the Grouse feeds more or less all day; but, as a rule, the crop is found fullest in the evening. Probably digestion is sufficiently rapid during the day to deal with the food almost as fast as it is picked and swallowed. It may be that the cæcum receives matter both by day and by night, and discharges its contents only in the early hours of the morning; but these details are not easy to determine in the wild bird, though it is easy to see how indispensable it is to the well-being of the Grouse that the cæca, whose combined length nearly equals that of the rest of the alimentary tract, and which are responsible for the absorption of most of its food, should be in good working order. It seems impossible to exaggerate their importance in the bird's economy, for if they are put out of action the bird may eat as much as ever and yet rapidly lose flesh by sheer starvation. It may suffer even worse things owing to the decomposition of the food and the diminished powers of selection during absorption, thus causing toxæmia. That this happens is evident, for it is a very usual occurrence to find the cæca in a case of Strongylosis, completely filled by a semi-dried mass of foul, cæcal matter adhering to the mucosa, leaving very little room down the centre for the passage of anything at all. In such cases the *Trichostrongylus* is usually excessively abundant, and may be seen bridging the space by hundreds between the adherent fæcal mass and the mucosa from which the latter is being forcibly separated in dissection.

Feeding
times of
Grouse.

Importance
of cæca.

Danger of
toxæmia.

*Tricho-
strongylus.*

One portion of the alimentary canal remains to be mentioned, namely, the rectum (Pls. XXVI. (R.), XXVII., Fig. 1 (*h*), XLIV.) This measures but $4\frac{1}{2}$ to 5 inches (=115 to 127 mm.) from the point of entrance of the Rectum. cæcal appendices to the anus. The internal appearance of the normal healthy rectum is shown on Pl. XXIX., Fig. 2; in this figure the dark staining about the cæcal orifice is due to the proximity of the liver.

The rectum appears to evacuate its contents almost immediately after receiving anything from the main gut or the cæca. When examined by dissection it is generally empty, or at the most but sparingly occupied by material; but there is one marked exception to this statement. In the hen Grouse, during the laying of eggs and incubation, but especially during incubation, the want of exercise, and the necessity for keeping the nest clean, leads to an excessive accumulation of fæces, always of the harder, formed kind, in the lower part of the rectum.

There is a great increase of size and of development in the ovary and oviduct in the breeding hen Grouse, and the rectum appears to accommodate itself to this. The massed and bulky droppings of a sitting hen Grouse, or "clocker" as she is called, are well known to the gamekeeper as affording the most reliable and useful information he can have concerning the number of nests upon his moor. These droppings, due to want of exercise and the brooding instinct, result in an enlargement and distention of the lower part of the rectum and the cloaca, which recover themselves only after incubation and hatching are completed.

As these bulky "clocker's" droppings are only to be seen on the moor in the nesting season, it is perhaps not surprising that the keeper alone recognises what they mean. It is a very common thing for a keeper to congratulate himself upon their abundance along the side of every burn he comes to. Such places are used habitually by sitting hens when they leave their nests, perhaps once or twice a day, for food and water, and these droppings supply far more satisfactory evidence than could be gained by disturbing the birds on their nests.

This then is, as briefly as possibly, the normal course of the digestion and absorption of food in the alimentary tract of the Red Grouse, and it remains now to speak of the more common pathological variations and disturbances which affect this process and which upset the health of the bird.

Variations
affecting
digestive
process.

Many such variations have come to light during the past five years in the course of dissecting something like a couple of thousand Grouse: of these some were healthy and some unhealthy; but in this chapter no account is given of lesions resulting from shot wounds or collision with wire fences or similar accidents. This subject is dealt with in another chapter.¹

By far the more important pathological changes which are to be found in the Red Grouse are those which result from excessive parasitism, and they are therefore discoverable as a rule in the intestines, and above all in the two blind cæcal appendices, which afford a habitat to thousands of the round-worm *Trichostrongylus pergracilis*. The particular cæcal lesion, connected with this threadworm, and with the fatal Grouse disorder which is now called Strongylosis, will be dealt with separately.²

Parasitism
the most
important
factor.

It will best serve the purpose in view to take again the alimentary tract from end to end, and to mention the lesions to which the various parts are liable.³

It is a very rare thing to find any disturbance in the upper reaches of the alimentary canal. The mouth, the œsophagus, the crop, the proventriculus, and the gizzard as a rule carry no entozoa, and are very seldom the seat of any pathological trouble. But it may happen that a bird gets hold of some irritant poison with its food, and this probably accounts for one or two otherwise unaccountable cases of inflammation of the crop walls, with engorgement and enlargement of all the vessels ramifying over it, and desquamation of the lining membrane (*e.g.*, Nos. 1611 and 1759).

In one bird (No. 1703) the crop contained plenty of fresh green *Calluna* tops, with Blaeberry leaves and bits of *Potentilla*, mixed up with abundant legs of the crane fly, all perfectly normal and wholesome foods, but the wall of the crop was excessively inflamed, the lining membrane shed, and a roughened surface was left exposed; there was much fluid mucus, and all the vessels were injected and engorged. There was also thickening of a granular appearance in the lower third of the œsophagus; but the mouth, throat, and trachea were all healthy. The mesenteric vessels were engorged and varicose, and the bird, which was a cock, and a bad case of Strongylosis, was infested with both kinds of tapeworm, weighed 15 ounces only, and was found dead.

Inflamma-
tion of
crop.

¹ *Vide* chap. ix. p. 153 *et seq.*

² *Vide* chap. x. p. 207.

³ *Vide* Diagram, p. 290.

Again, No. 1846 was a hen Grouse of 15 ounces only, found dead on May 6th, 1909, in Perthshire. This bird was very backward both in moult and in the development of the ovary. There was no attempt to put on the nesting plumage. But the cause of death was an excessive repletion of the lower œsophagus and proventriculus. From the level of the base of the heart to the point of admission to the gizzard the mass of food in the œsophagus and proventriculus formed a uniform sausage-shaped mass, which seems to have caused death by pressure upon the heart within the thorax. Why this collection of food should have failed to find its way into the gizzard it is impossible to say. Mechanical obstruction there was none, either by unusual food or by stricture. These were at once looked for without success. Some spasmodic stricture of the entrant sphincter muscle of the gizzard may have accounted for this, though there was no direct evidence of it. The gizzard and its contents were perfectly normal, and there was apparently free passage both in and out of it. The crop contents were unusually moist with water and watery mucus. They consisted only of green *Calluna* heather-tops, but there was a much smaller quantity in the crop than in the proventriculus. There was no appearance of damage by shot or other means, such as might account for paralysis of the lower œsophagus, though this would, perhaps, be a plausible explanation, as the damage done to a nerve in the neck by a stray pellet could have been healed without leaving any noticeable scar, and yet the nerve remain severed, thus putting out of action the parts it supplied.

No. 1311, a hen Grouse of $16\frac{1}{4}$ ounces found dead on March 30th, 1908, in Perthshire, was a case presenting almost exactly the same appearances as the above, and with no clearer evidence of its cause. This bird was very thin, and was found not far from a dead grey-hen; but the grey-hen showed no sign of similar trouble. In this Grouse the crop contained a small amount of large pieces of woody *Calluna* heather. The proventriculus was perhaps a little swollen, but the lower half of the œsophagus was intensely engorged with food, making again a sausage-shaped swelling within the thorax, which must have exerted a fatal pressure upon the heart and blood-vessels. The bird was not suffering from Strongylosis to any noticeable extent, that is, the cæcal villi were not engorged.

It is a possible solution that the crop having received something irritating in the food, acted suddenly and completely, emptying itself into the

oesophagus, and thus paralysing this part of the alimentary tract by over-distension. The contents were not examined for irritant poison, but the birds might possibly obtain some such poison if they fed off heather which had been contaminated by sheep dip in dry weather. This, however, is not probable in March.

In the duodenum it is comparatively common to find the mucosa intensely engorged, showing a bright red surface to the naked eye, sometimes all over, and at other times in patches. This is apparently the result sometimes of the presence of *Hymenolepis microps*, in large numbers; sometimes of the presence of *Trichosoma longicolle*. Such a mucosa, seen under the lower powers of the microscope, shows that the vessels of the villi are all full of blood as shown in the accompanying figures (see Pl. XXVIII., Figs. 4 and 4 (a)); but although in many cases the mucosa is thus reddened and *Hymenolepis* and *Trichosoma* are abundant, it is also quite as frequently found that the worms are present without any reddening, and in some cases reddening is present without any sign of a worm. Nevertheless one very common association in the duodenum, whether it has anything to do with cause and effect or not, is that in one and the same bird *Hymenolepis* occurs in very large numbers, the villi are densely injected, and the fluid bathing the worms has the appearance of being bloody (see Pl. XXVIII., Fig. 2).

Engorge-
ment in
duodenum.

Cause may
be thread-
worms or
tape-
worms,

For example, in No. 1200, weighing $21\frac{1}{2}$ ounces, found sick, the duodenum was of a deep red both inside and out, the villi all injected, the mesenteric vessels all engorged, and *Hymenolepis* was present. The bird had, however, been feeding on corn, and it is possible either that the siliceous spicules of the oats were the cause of much irritation, or that the general venous engorgement resulted from the Strongylosis which was also present.

Or corn-
feeding.

It is also probable that in many of these cases where there is villous engorgement and redness of the mucosa in the duodenum and smaller intestine, Coccidia have been the cause and have been overlooked, and that the more obvious threadworms (*Trichosoma*) have really little or nothing to do with the engorgement.

Or
Coccidia.

It may exonerate *Hymenolepis* and *Davainea* to some extent, that both may be present in masses without any accompanying congestion, but the occurrence of a large number of *Trichosoma longicolle* in the duodenum, associated with an accompanying congestion of the mucosa, and the presence in the gut of dark bloody-looking fluid is too frequent to allow this

nematode to escape blameless in the company of the two above-mentioned cestodes. *Trichosoma* is probably a harmful worm, but as it seldom occurs, as compared with the frequency of *Trichostrongylus* in the cæcum, the damage done by it is comparatively trifling.

In the duodenum then it is possible to have *Hymenolepis* present in large numbers with or without engorgement of the villi, but when, as in No. 1525, *Hymenolepis* occupies no less than 8 inches of intestine, extending from the duodenum for several inches into the small intestine, the villi may be excessively congested. In such a case, moreover, as in No. 1864, if the bird has Strongylosis the congestion of the mesenteric vessels seems to affect the

Effect of
congestion
in appear-
ance of
duode-
num.

appearance of the duodenum also. Normally the duodenum and the pancreas are pale creamy pink or white with no visible external blood-vessels; but this is altered under conditions producing congestion, to a deep red or bright purple or crimson colour over which the engorged vessels ramify (see Pl. xxviii., Fig. 2).

As already stated, the villi of the duodenum may be occasionally found in a state of excessive redness, with apparently no trace of a worm of any kind. Such a case was No. 1391, but it was also a very bad case of Strongylosis in a hen found dead, so the change may have been *post-mortem* only, or it may have formed part of a more general congestion.

Typically the duodenum when badly infested by *Hymenolepis* looks bulky and translucent, swollen and soft and is of a pinkish yellow colour, with thin walls. The upper end of the ascending limb is often deeply stained by contact with the liver. The contents besides the *Hymenolepis* are fat globules, no crystals, as a rule, but an abundance of shed, endothelial cells. The fluid contents, always small in amount, of the duodenum are generally yellowish, and may be blood-stained if *Hymenolepis* and *Trichosoma* are present in excessive numbers.

It is not a rare thing to find that in a sick bird the control of the lower sphincter of the gizzard is lost at the point of death or somewhat earlier, and

Grits. that the grits have passed out of the organ in large quantities into the duodenum. Normally the grits are retained in the gizzard for a considerable time, certainly for months, if they are of any size. Much depends upon the nature of the food, and as already explained the presence of hard, woody seeds may lead to the loss of most of the gizzard grits, in which case they are passed with the dejecta.¹

¹ Vide p. 97.

PLATE XXIX.

Rectum Villi of Fig. 5 magnified under 5 inch obj.



Fig. 6.

Typical appearance of small Intestine when filled with *D. calva*.

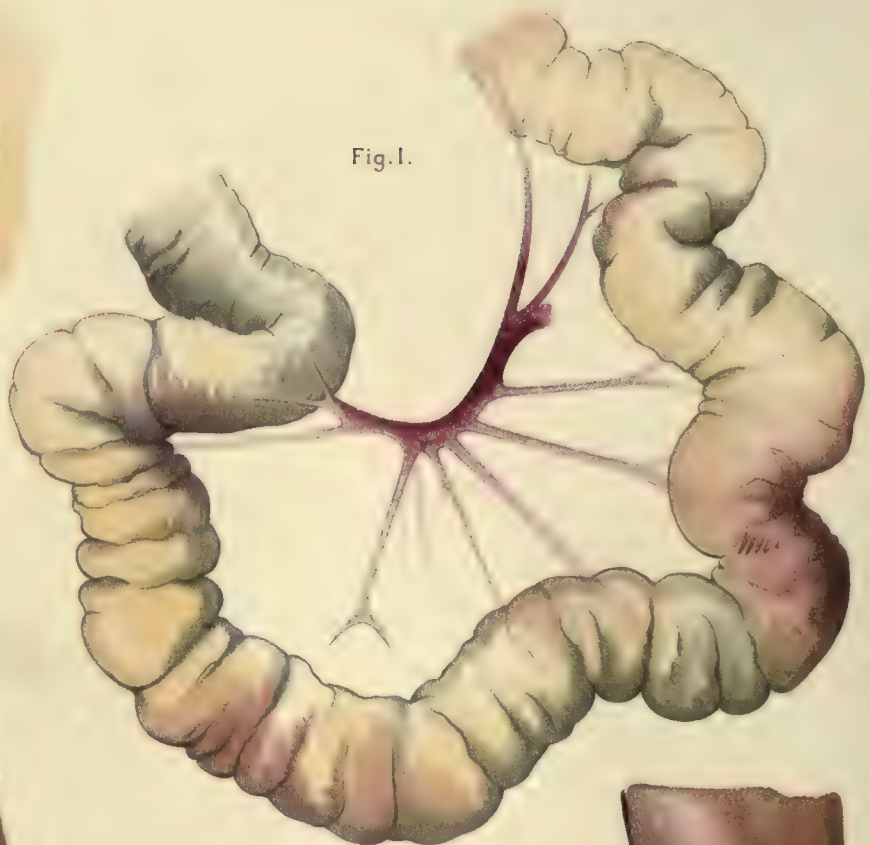


Fig. 1.

Rectum Posterior third very much inflamed.

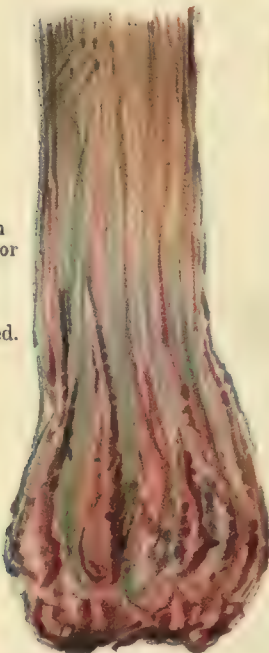


Fig. 4.

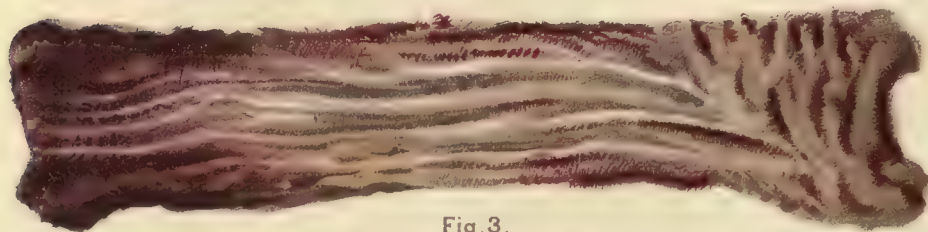


Fig. 3.
Rectum, inflamed condition.



Fig. 5.

Rectum, punctiform infection of villi.

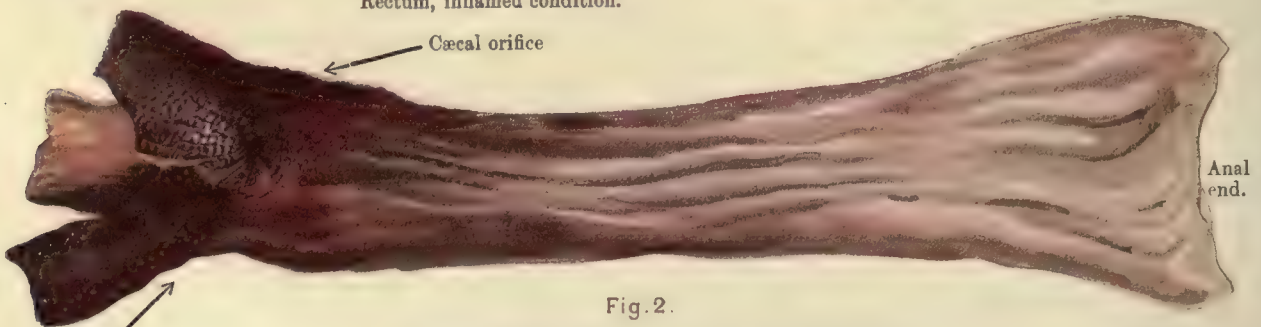


Fig. 2.

Rectum normal or nearly so; the dark staining about the caecal orifice is due to the proximity of the liver.

Anal end.

Caecum cut open longitudinally

F. Wilson, Cambridge

Passing now to a consideration of the small intestine, and its pathological manifestations, the first noticeable point is its external appearance when really full of *Davainea calva*, as is so frequently the case (see Plate XXIX., Fig. 1); the gut is distended, and appears fatty, thin-skinned, yellow in colour, and rather translucent. Within, there are often great masses of *Davainea*, but no redness of the mucous membrane. Small intestine.

In No. 1219, a cock Grouse of 21 ounces, found dead, the whole of the lower straight portion of the small intestine was enormously distended with food not long eaten. The crop contained *Calluna* tops, a few insects and some seed-heads of a *Ranunculus*. The gizzard contained plenty of quartz and food; the duodenum contained *Hymenolepis*; and the upper small intestine a few *Davainea*. The cæca were almost empty, and although no obstruction was visible there was obviously something preventing the admission of food to the cæca from the lower main gut. The distended intestine measured nearly $2\frac{1}{2}$ inches round, and the thickening of its walls showed that the condition was not merely temporary. The mucous surface was roughened with greyish-white, swollen mucous glands which may have been the cause of the trouble, since they probably failed to supply sufficient moisture to the food for its passage into the cæca. It was a condition analogous to excessive and prolonged constipation, and it is evidently a rare condition in the Grouse, for no other case like it has been seen. Obstruction of the small intestine.

A punctiform pigmentation of the serous surface of the small intestine is not uncommon. It occurs in small areas which are thickly dotted with black pigment. Probably it results from a previous inflammatory condition, or small localised peritonitis, which may possibly have been caused by the masses of *Davainea* within the gut. Grouse No. 1182 and No. 1739 are good examples of this condition. In the latter the pigmentation was more or less generally distributed over the serous covering of the cæca as well as of the small intestine, and as the bird had been wounded by shot some considerable time before it was killed, there is a likelihood of the peritonitis having been more general than local, though there were enough worms and congestion in the intestines to account for the appearance. Pigmentation of surface.

It is not a common thing to find the small intestine acutely inflamed, or very red or congested, but in Grouse No. 1113 the straight portion was excessively red with orange-coloured mucus, evidently blood-stained, and a very large number of *Davainea*. This, however, was a Inflammation of intestine.

bad case of *Helminthiasis*, with intussusception; the cæca also were intensely congested and very much thickened, the lower third especially was blood-red, and full of *Trichostrongylus*. The duodenum also was much inflamed, and for a male the weight, $15\frac{3}{4}$ ounces, was, of course, exceedingly small, showing that it had suffered severely in its struggle with so many parasitic worms. Of this condition, therefore, one might expect well-marked *post-mortem* evidence. The intussusception was probably the result of great irritation.

The only pathological appearance which is commonly seen in the rectum of the Grouse is a reddening along the glandular ridges, due to villous engorgement. This appearance is illustrated on Pl. XXIX. where Fig. 2 shows the rectum in a normal healthy condition. Fig. 3 shows the same when inflamed throughout its length. Fig. 4 shows the rectum with the posterior third very much inflamed. Fig. 5 represents the punctiform injection of the villi, while Fig. 6 shows the same injection when magnified under a 1-inch objective. The cause of this villous engorgement is obscure, but it is much more frequently found about the lower third of this portion of the gut than about the upper two-thirds, though it may be general throughout the rectum. It does not appear to be dependent upon disease or sickness, though apparently sometimes it has some relation with an excessive number of tapeworms in the main gut.

In the cæca of the Grouse lies the whole origin and cause of "Grouse Disease" in the adult bird. In these blind guts lives *Trichostrongylus pergracilis*, and these, when present in enormous numbers, produce an excessive amount of irritation and congestion of the vessels and of the capillaries in the villi, desquamation of the endothelium, and so much disturbance of the proper functions of this portion of the gut that the contents, consisting of food, mucus, nematode worms, and nematode ova in a pasty and decomposing mess, not only become useless as food, but a grave danger to the bird owing to the amount of toxins produced and absorbed into the circulation. The internal appearance of the normal cæcal mucosa is shown on Pl. xxx., Fig. 1, which represents a section of the cæcum of a healthy bird; the nodules and granular ridges are yellowish, and the interstices are dark reddish brown. The external appearance of the normal healthy cæcum as it lies in the body of the Grouse is seen in Pl. xxvii., Fig. 1 (i). But when badly

Inflamma-
tion of
rectum.

Cæcum.

*Tricho-
strongylus.*

PLATE XXX.



infested with *Trichostrongylus* both the external and the internal appearance become quite altered (see Pl. xxx., Figs. 2, 3, 4, and Figs. 5, 6, 7, 8, 9). In this Plate, Fig. 2 shows the cæcum much swollen with the mucosa thickened and congested, and the mesenteric vessels engorged, the mucosa show a little red, punctiform inflammation from the injected villi, otherwise the colour is grey and the ridges are tumid and much swollen. Figs. 3 and 4 show the cæca much congested, and the mesenteric vessels engorged with dark venous blood. Fig. 5 represents an exceptional appearance, the four greater and four lesser ridges are well defined, there is no trace of nodules, but there is slight inflammation. Fig. 6 shows the interior of the lower end of the cæcum, and Fig. 7 shows a section of the middle third, in both these examples the mucous membrane is much congested, and hypertrophied with fully injected red villi. Figs. 8 and 9 show the appearances in a bad case of Strongylosis.

Other extreme cases of Strongylosis are shown on Pl. xxxi., where Fig. 1 represents a portion of the cæcum at the junction of the lower and middle thirds. Fig. 2 shows a similar appearance in the middle third. Fig. 3 illustrates a section of the first third intensely congested, while Fig. 4 shows the same when magnified under a 1-inch objective. In Fig. 5, showing a section between the lower and middle third, there are large spaces with no trace of ridges; but it is probable that this is the effect of *post-mortem* change.

Instead of an intestine of a brownish or greenish grey colour moderately filled with soft brown pasty material, and showing greyish yellow lines running down its length on the outside, indicating the eight or nine long villous ridges within, we see in the cæcum of a diseased bird a distended tube, with overfull and congested blood-vessels ramifying over it on the outside, standing out very often in conspicuous contrast with a yellowish fatty-looking gut-wall; or the whole substance of the wall of the cæcum may be congested to a deeper tone, and may look dark, blue-black, and unhealthy. Before opening the gut, however, the congestion of the mesenteric vessels is the most conspicuous point. This is due to a venous congestion, and it means that the liver and other abdominal viscera and the right side of the heart are overfull. The liver may be very dark. It decomposes rapidly, becoming of a black, tarry, soft and very rotten consistency; but this is not a safe indication of disease. The difference in appearance between a healthy liver during decomposition and a diseased liver is so uncertain that, after a day or two of summer heat, it becomes impossible to judge whether

Appear-
ance of
unhealthy
cæca.

Liver and
heart.

the bird was diseased or not. The right side of the heart is often enormously distended with black blood in a bird that has died of disease. This condition of the heart, however, must not be taken as necessarily present when the cæcum is diseased.

When the caeca of a large number of Grouse, all more or less suffering from Strongylosis, are opened up and examined in various stages of freshness, and in some cases after a lapse of many days since death took place, the appearances are very variable.

In some birds the upper portions of the cæcum are almost transparent (see Pl. xxxi., Fig. 6), but this transparency is certainly increased by the *post-mortem* maceration of the mucosa. The longitudinal ridges, moreover, gradually diminish in breadth and in villosity as the blind end is approached. The thickenings so conspicuous in some birds are far more abundant at and towards the open end. The ridges are sometimes very obviously alternately large and small, giving four broad and thick and four narrow and thin (see Pl. xxx., Fig. 5).

In bad cases the villi are intensely congested, and in a certain number of cases there is evidence of hæmorrhage having taken place here and there. But extensive hæmorrhage does not occur in Strongylosis, or at any rate no indication of extensive hæmorrhage has been seen in any bird dissected. The reasons which lead to the belief that there is always a loss of blood as a chronic symptom in this disease are that the congestion is always present, and is often excessive; that small hæmorrhages have been seen, and that in some advanced cases there is every appearance that one would expect to find in anæmia in a bird. It must be allowed that without Dr Fantham's blood examinations this would be an insufficient explanation. In some birds the pale, bloodless, fatty and degenerated aspect of the tissues of the internal organs was most suggestive of anæmia, and of chronic toxæmia.

It is possible to find quite a number of very healthy looking birds with good weights and yet with a large number of *Trichostrongylus* and a considerable amount of villous reddening. This goes without saying in such a disease as Strongylosis, which is essentially a progressive ailment.

Everything depends upon the strength of the bird, and its power of resistance. There is no doubt that some birds will retain their weight and continue for some time in apparently perfect health, with a very great number of *Trichostrongylus* in the cæca, and a considerable amount of con-

*Tricho-
strongylus*
in healthy
birds.

THE
OF
CALIFORNIA

Fig 1



Fig 2



Fig. 7.



Fig. 8



Fig. 3.

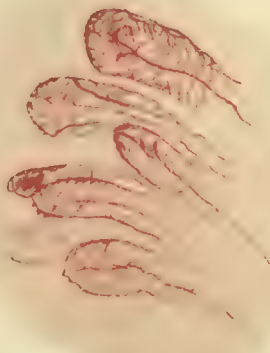


Fig 4

TRANSPARENT
INTESTINE

Fig 6.



Fig 5.

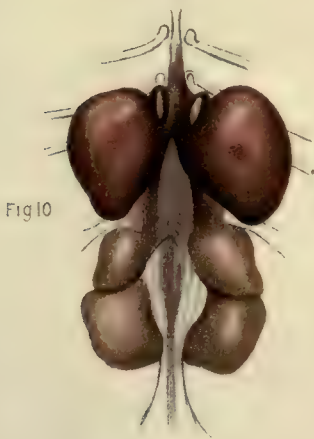
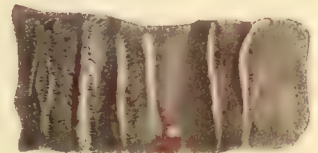


Fig 10



Fig 9

E Wilson, Cambridge

gestion. There is also little doubt that an observer may be easily misled by a physiological redness of the cæcal villi due to normal processes of digestion. This is especially the case if the bird examined happens to have been in the middle of this process at the moment of death, and if death occurs without loss of blood. The abdominal viscera must all be more full of blood at that time than at others, though in a bird like the Grouse which eats all day long, the difference may be less marked than it would be in ourselves or in birds of prey which feed at longer intervals.

The chief signs of a bad case of Strongylosis so far as the cæcum is concerned are:—

Signs of
Strongy-
losis.

(1.) An excessive number of the worms, which can be seen stringing across between the mucosa and the caked contents of the gut, if the contents are fairly dry. If not, then, by taking a small quantity of the pultaceous contents and squeezing this flat between two glass sides, the worms can be easily seen as transparent threads when held up to the light. Innumerable ova will also be found lying free in the cæcal contents.

(2.) The longitudinal ridges, eight to nine in number, are very much thickened, chiefly because the amount of blood held by them is excessive, and the villi are all engorged.

(3.) The swellings shown in Pl. xxx. (Fig. 1), and conspicuous in a healthy bird as greyish nodules, are far more conspicuous in a case of Strongylosis when they are reddened and congested, and seem to suffer to a greater extent and earlier than the remainder of the ridges and the rest of the cæcum (*see* Plate xxx., Figs. 6 and 7). In some cases, however, the time comes when every villus in the whole gut seems to be intensely red and congested from one end to the other (*see* Figs. 8 and 9).

(4.) There may be a very great deal of mucous thickening, from the swelling up of the villi and their columnar epithelium cells, and after maceration *post-mortem*, the cæcal mucosa seen in water may have the appearance of a furry rug. The mucous contents of such cæca are sometimes obviously blood-stained, and there is probably a hæmorrhagic form of the disease which results from the sudden access to the gut of a very great number of larval worms all in a fully metamorphosed state. Such a case was produced experimentally at Frimley, and hæmorrhages occurred in the cæca. There is no apparent reason why under certain easily imagined circumstances the same thing might not happen in early springtime under natural conditions.

(5.) There may be appearances of recovery. In a good many birds the caecal mucosa is dotted all over with minute black pigment granules, in other words some of the villi show no blood-vessels injected, but are filled with pigment granules instead. These are sometimes so abundant as to colour the gut. They lie in the villi in great numbers (see Plate xxxi., Figs. 7 and 8).

It is possible that they result from previous chronic congestion and that there are circumstances under which the bird may rid itself of an excessive number of *Trichostrongylus*. If there is any plant which acts as a vermifuge to this nematode on the Grouse moor, and if it could be discovered and encouraged to grow one cannot help thinking that the Grouse might learn to eat it. If this supposed recovery from Strongylosis has not resulted from some unknown vermifuge herb, then it must have resulted from improved conditions of life; and the one condition of life which is in the hands of the moor proprietor is the food supply. It thus becomes imperative to give every Grouse on the moor the best possible chance of overcoming the parasitic pest which produces what is probably the most harmful feature of the disease, namely the chronic congestion of the villi of the caeca. Improve the conditions of life, improve the circulation so that the heart and lungs work more efficiently, and the digestion automatically improves, as also does the elimination of toxins, whether produced by the parasitic worms, or by the food eaten, or by bacteria in the gut. The worms, one must suppose, remain in the gut; but the congestion is overcome, and the bird is not very much the worse for their presence. But, if the congestion is allowed to continue and become chronic, the digestion and absorption of food must go from bad to worse, and with it every other function of the body. Nothing will prevent the bird in this case from losing its weight, and eventually its life.

As for the exact cause of the congestion, it may be due to mechanical constriction of the filamentous processes of the villi by the nematode worms.

The immediate cause of congestion. Each time the gut acts peristaltically the worms have to hold on tightly to the mucosa or else be dislodged with the dejecta, and the result is seen in sections where the villi are evidently mixed up inextricably with the coils of *Trichostrongylus*. Or it may be due to the chemical irritation of some poison produced in the gut by the worms, or by the defective digestion of food stuffs, or by bacteria living in the gut in its unwholesome state. Or it may be due to some or all of these conditions together.

On the whole the mechanical view seems the most probable. The peristalsis is acting in a way to dislodge the worm, and the *Trichostrongylus* has no other way of retaining its position in the cæca save by coiling round something, and the peristaltic action of the cæcum must be fairly strong in comparison with the strength of the worm, for the free end of the worm has to be released at every wave of peristalsis from immersion in a thick, pasty material which is being driven outwards at each contraction of the gut. It thus seems evident that the small and delicate processes of the villi may be continually on the stretch, at first looped round tightly by a worm, the coil may then relax, blood may enter the capillaries, only to be compressed anew and so on, conditions which cannot but produce congestion on a large scale if multiplied a sufficient number of times.

So far as the appearance of the cæcum in disease (Strongylosis) is concerned, the following rough, laboratory notes describe some of the types:—

Examples
of Strongy-
losis.

(No. 1908.) Found sick. The cæcal mucosa not very red, but whitish, pale, the cæca full of mucus, and innumerable *Trichostrongylus*. Congestion apparent in the mesenteric vessels but no marked villous engorgement, only mucus in excess.

(No. 1875.) *Trichostrongylus* very abundant, but no excessive amount of villous engorgement. Contents of cæca almost nil, this may account for subsidence of engorgement and reduction of redness.

(No. 1854.) Cæca very badly engorged at lower open ends, but less towards centre. The whole gut swollen, foul and unwholesome, and *Trichostrongylus* very abundant.

(No. 1844.) Cæca much swollen and very full of material. Excessive villous congestion and redness. Abundant *Trichostrongylus*. A hard concretion at the blind end of one cæcum shows that matter may remain there sometimes for lengthy periods. The whole venous system intensely congested, and the swellings on the cæcal ridges exceptionally red with engorged villi.

(No. 1842.) Cæca very much swollen, villous redness much marked, and very deep in colour. The whole contents lumpy and irregular, soft and hard, partly dried up, so that from without whitish lumps showed through.

(No. 1839.) Cæca very large and unhealthy, thick with whitish mucus. Red

engorged villi showing up against white fatty-degenerated mucosa and gut walls. *Trichostrongylus* very abundant.

(No. 1728.) Villi red and engorged with blood from one end of the cæca to the other, and the redness especially marked on the swellings along the longitudinal ridges.

(No. 1914.) Cæca swollen with mucus, pale and translucent. Only a few red villi, but very large numbers of *Trichostrongylus*, and innumerable ova.

(No. 1215.) Very full of shed mucous cells, or unwholesome, yellow mess, but no active inflammation. Plenty of pigmentation in minute dots. *Trichostrongylus* very abundant.

(No. 1827.) A very unhealthy swollen condition with villi uniformly congested and red throughout. *Trichostrongylus* very abundant. Contents of cæca clotted and adherent. No redness except in the cæca, though both cestodes were present in some numbers.

(No. 1747.) Cæca with excessive numbers of *Trichostrongylus*; very swollen and full of clotted, tenacious, and bloody mucus. The whole gut excessively unwholesome, large and congested with red villi partly macerated, and their cells being shed. Adhesions—probably *post-mortem*, due to crystalline precipitate in the serous fluid—were to be found all along the cæcal mesenteries and peritoneum.

(No. 1727.) Cæca very pale, but with red villi engorged throughout.

(No. 1602.) No red villi, but excessively unwholesome contents almost dry and very hard in the centre. *Trichostrongylus* in excessive numbers; both cæca very much distended, pale and swollen with mucus. The mesenteric vessels all congested.

(No. 1369.) Cæca full of stiff orange - coloured mucus, beneath which the gut is thin, red, and inflamed in appearance.

Many of these cæca in diseased birds are very thin and red in the middle and upper ends, while the lower open ends contain innumerable red villi. Often it appeared as if not only cells but villi and parts of the mucosa have been shed or detached, perhaps because the mechanical strangulating movements of the *Trichostrongylus* leave little but the basement-membrane and the wall of the gut, which are there almost transparent.

One abnormality occurred in connection with one cæcum of No. 1266, namely, an intussusception of the free blind end which has a free mesentery. It was

involved in the attached portion of the cæcum until only a portion of the blind end remained visible, and this was black and gangrenous, or nearly so. There was very little sign of Strongylosis. The bird was shot, and was in good condition.

With regard to other organs of the body of the Grouse there is more to be said of the lungs than of any other. On this subject the reader may be referred to chapter xii., where Dr Cobbett and Dr Graham Smith have described in detail the appearance of really fresh lungs, exposed in birds just dead, and their appearance after being more or less stained by *post-mortem* fluids and decomposing blood.

Pathology
of the
Lungs.

The figures which were prepared with the view of illustrating this difference could not be reproduced in the Report owing to lack of funds.

The first series of figures represented the lungs of fourteen Grouse removed at various periods of time after death, and showing marked staining of the tissues. The second series represented the lungs of eight pigeons removed also at various periods after death, and showed the same or very similar staining in all cases where the lungs were allowed to soak in blood-stained, *post-mortem* fluids, as is the case in the majority of Grouse which have been shot or bruised, or even carried for many hours over a rough moor in a keeper's pocket or net bag. Even without preliminary bruising or damage there will be found a certain amount of soaking and discoloration of the lung tissues after death.

Appear-
ances in
lung due to
post-mortem
change.

In very bad cases of *Strongylosis*, such, for example, as No. 1228, the lungs even on the third day after death may be perfectly normal in appearance, and without any marked *post-mortem* staining. The lungs of birds may, of course, have received some damage, either by shot pellets or by broken bone splinters, and may have recovered with cicatrices, or with part of the lung solidified by organisation of the blood clot into fibrous tissue. Or blood may have been inhaled by the trachea, and so have blocked part of the lung, producing collapse and solidification.

It is wise, in every case when a bird is found dead, to examine the mouth and see whether there has been any bleeding from the lungs.

It is unnecessary here to repeat the discussion upon the question of "Grouse Disease" and pneumonia. For this reference must be made to chapter ix., where reasons are given in full for the belief that Klein's explanation of "Grouse Disease" as an acute infectious pneumonia is not the correct one.

"Grouse
Disease"
and pneu-
monia.

The normal colour of quite fresh healthy lung is a very clear pink, almost a whitish pink until the organ is cut into when it is found to exude bright red blood, and the cut surface therefore immediately becomes bright red.

Lung quite healthy in diseased birds.

The appearance of fresh lung in bad cases of *Strongylosis* does not, according to our experience during the past six years, vary at all from the appearance of the lung in health, and there is no sign of solidification or of the earlier stages of pneumonia, congestion, or infiltration in the lung as a symptom of the disease.

Pneumonia proper must be an exceedingly rare disease in the Grouse, and probably ninety-nine out of every hundred diagnoses of it are the result of a failure to realise that *post-mortem* staining and infiltration give an appearance which may be mistaken for pneumonia. But it is exceedingly difficult to find even a very small piece of this so-called pneumonic lung which will not float in water, and this is a fairly reliable rough-and-ready test for consolidation.

In Grouse No. 1260 small caseous masses were found in several portions of the lung, and also adhesions to adjacent parts, but it was found on examination that two ribs had been broken on each side and had reunited, showing that a pellet or two of shot must have been the cause of the damage to the lung, which (apart from the remains of a small localised abscess here and there) was of a typically healthy colour and appearance. The condition of some very much enlarged veins ramifying over the surface of the proventriculus in this bird, which were probably taking upon themselves the duty of vessels previously damaged and obliterated by the accident which broke the ribs, are described elsewhere (*see* p. 166).

In one or two rare cases (Grouse Nos. 899 and 900), as the result of a continued search under high power amongst the débris and fluid procured from a crushed piece of lung, a living larval nematode has been discovered in active movement. This was in a lung which had every appearance of perfect health both in colour and consistence, and yet was taken from a bird so sick of *Strongylosis* that flight was impossible. A lung such as this, which is a bright, normal, pink colour when the bird quite recently dead is opened (in the case in point the bird died in the hand and was at once examined), may yet in twenty - four hours be so much altered as to have a very deep gelatinous, patchy redness throughout. Later still some parts will turn almost black, while others remain pale; and the observer who then sees the lung for the first time is almost certain to suspect some

Parasites sometimes found in lung.

pneumonic change in the tissue. As a matter of fact, however, the change is at first superficial, and is more pronounced where the lung is in contact with the liver. The staining gradually makes its way, *post-mortem*, into the body of the lung, so that in a few days a section shows fluid containing degenerating and decomposing corpuscular debris which has leaked into the air spaces and has produced the condition illustrated and described before now as the second stage of pneumonia in Grouse. At this stage the colonies of bacteria block the blood capillaries and form a characteristic feature; *but* this is a *post-mortem* feature.

With regard to the liver there is very little to be said. It is an organ which changes perhaps more rapidly *post-mortem* than any other, both in appearance and in consistence, and yet more has been deduced from its *post-mortem* appearance than from any of the more reliable indications of disease Liver. in Grouse. If the liver be examined fresh, even from a bad case of Strongylosis, it will be found to present a normally firm consistence and a healthy red colour. It is true that it may, and probably always will, partake of the general and at times localised abdominal congestion which characterises Strongylosis. But this alters its normal appearance very little *when it is fresh*, it may be a slightly darker red, and it may be a little more friable, but the change is hardly noticeable. The "black" and "tarry" livers may be ignored, unless they occur in birds that have only quite recently died, as being indications of no value from the diagnostic point of view. The staining even in a fairly fresh liver will often be found upon section to be very superficial and to be creeping towards the centre from the liver surface to the interior. Hence the first portion to show the change right through is always the edge of the anterior lobes.

The only examples of disease affecting the liver of birds which have been examined by the Committee were cases of Coccidiosis, and even then the connection with Coccidiosis could not be established with certainty as the specimens referred to were also cases of recovery from wounds or mechanical damage.

Small areas of fatty degeneration and localised necrosis have been seen in one or two cases, but have no apparent connection with Strongylosis. The liver in cases of Strongylosis may be considered valueless, from a diagnostic point of view, so far as macroscopic signs go. Microscopically it has been shown to be possibly of more importance (*see* chapter xii.), and the changes to be found *post-mortem* are fully described by Professor Klein in his work on "Grouse Disease."

The spleen of the Grouse varies very much in size, and this fact appears to have some connection with Strongylosis. It is comparatively large in young and healthy birds, and is large, as a rule, and of a fresh, red colour in healthy adult birds; but in cases of Strongylosis it becomes very small and very dark, an appearance which is noticeable in fresh, dead cases of disease, and even more noticeable as *post-mortem* changes advance.

The colour of the kidney in a freshly killed healthy bird is a reddish brown, a good deal paler than the colour of the liver. Normally the lobes of the kidney lie very flat against the dorsal wall of the abdomen, fitting into the inequalities of the skeleton. Fig. 9 of Pl. XXXI. gives a rough sketch of the appearance of a normal healthy kidney as it lies *in situ*, with the testes overlying the upper lobe, one on each side.

The kidneys appear to suffer very little either from the general congestion which must be considered a symptom in Strongylosis or from their function in ridding the body of poisons which are probably to be found in the general circulation. Only twice has the kidney shown any macroscopic change, and in each case it was due to an enlargement which in Grouse 1292 affected every lobe, but in No. 1107 chiefly the upper lobe.

Case No. 1292 was a hen Grouse of 18 ounces found sick, and caught alive on 6th March 1908 in Yorkshire.

It was a very thin bird, and in very poor feather; it had Blaeberry shoots in the crop, no tapeworms in the duodenum or small intestine, but some Strongyles in the cæca, which were full of a dark greenish black slimy mess, like that which generally occupies the cæca of Blackgame, the result probably of a low ground diet of soft green leaves of clover, grass, and *Tormentilla*.

The liver was exceedingly dark, but not enlarged and with no spots. The spleen was small (9 mm. long) and black. The kidneys were much swollen, and were brown with black markings, in spots; but this colouring may have been due to *post-mortem* change.

Case No. 1107 appeared to be the result of acute inflammation, the upper lobe being exceedingly swollen and enlarged, and of a rich red colour (see Plate XXXI., Fig. 10). In this case it will be seen that the testes have been slightly displaced from their normal position owing to the swelling of the kidney.

Of these two cases, the first had been five days dead, and the other three, in August and *post-mortem* change had set in. The condition cannot be considered in any way directly connected with Strongylosis, or more than two cases would have been found in a series of nearly two thousand examined.

The testes appear often to run a normal course of development as the breeding season approaches, however seriously the bird may be diseased. The first sign of any increase in the size of the testes is to be found about the third week of February, at least in the northern half of Scotland. Further south it might be found a little earlier perhaps, but in 1908 for Banffshire the date was February 23rd, while for Durham it was February 24th. In May the testes have increased in size to twenty or thirty times the bulk they had during inactivity, and they are then white and fatty, whereas in winter they are generally small and black and deeply pigmented.

Testes.

Occasionally a very emaciated cock bird will be found with testes only half the normal size during the breeding season; but, as a rule, the effect of disease on the development of the hen's generative system, both ovary and oviduct, is far more noticeable than is the case in the male.

If we allow that the prenuptial moult has become post-nuptial in the male as a result of chronic parasitism, it is conceivable that the same saving of energy allows of this sexual development in the male; whereas in the female, in which the moult is prenuptial as it should be, there are no "savings" to fall back upon in the event of bad disease, and therefore the sexual development is unsupported, and none takes place.

It is very noticeable that in sick Grouse hens there is no development of the ovaries or enlargement of the oviduct and cloaca, such as takes place in spring in every healthy hen. The ovaries remain small and undeveloped as in midwinter. Such birds are barren if they pair, for as a rule they cannot lay an egg, but they pair nevertheless, as every gamekeeper knows to his cost in a bad year.

Ovaries.

Such birds are often very backward in their plumage change as well, suggesting that the time may come when the hens as well as the cocks may have to don the prenuptial dress when the breeding season is finished instead of before it, as is the custom with the hen Grouse now (see chapter iii. p. 45).

Plumage backward in diseased birds.

For example, Nos. 1878 and 1879 were two hen Grouse found dead of Strongylosis in May. One had put on the full breeding plumage, but was

not laying, and the ovaries were very small, dark, and wholly undeveloped. The other not only showed no development of the ovaries, but was still almost entirely in the winter plumage, having had no strength to grow the nuptial one. Such birds are always wretchedly thin, and these weighed 15 ounces and 16 ounces respectively.

We found many cases which showed that in the hen the plumage change must come first, for it often happens that (*e.g.*, Nos. 1864 and 1870) the breeding plumage is complete and excellent, even in wasted birds of $13\frac{1}{2}$ ounces and 14 ounces, whereas their ovaries are as undeveloped as in mid-winter.

The suggestion that such weakly hens may achieve a nuptial plumage by a re-arrangement of the pigment in their feathers without undergoing the drain required by new growth, cannot be adopted.

This difference between the male and the female Grouse is significant.

Difference
between
plumage
changes in
cock and
hen.

It seems that, in the male, appearance may be sacrificed to efficiency, whereas in the female appearance comes first, and the nuptial plumage is donned at any cost, often to the undoing of the hen herself, at any rate to the complete undoing of her power to produce an egg.

There must, of course, be many sickly hens that not only don the breeding dress but also lay a modicum of eggs. They appear later in the shooting season with every sign of disease and exhaustion upon them, but yet recovering.

Grouse that have survived the mortality of April and of May do not die later in the year. They become convalescent through the summer and autumn,

Sick
Grouse in
August are
con-
valescent.

owing to good food and better weather. There is no autumnal, mortal outbreak of disease; but there is an increased activity in the collection of birds that have been sick and are convalescent. These birds can fly, and are shot in August and September; it is only when they are discovered in the bag, in the process of sorting later in the day, that they are suspected of disease, and are forwarded to the Committee for examination.

Such birds are not at the point of death, but are, in fact, convalescent. They are not the birds that will be killed off necessarily in the coming winter, but may perhaps be still weaklings in the following spring. They are the birds that in the *previous* spring were badly hit by Strongylosis, but managed to survive April and May, and then were safe with a supply of good and varied food assured to them for at least eight months to come.¹

¹ *Vide* chap. iv. p. 72.

As we know much about these wasted autumn hens it is now safe to say that they may be placed in two classes:—

- (1) Those that were too sick in the spring to breed at all, and so remained barren.
- (2) Those that were not too sick to breed, but bred small clutches and reared from two to four or five young Grouse.

History of
autumn
pining
hens.

The first class has the best chance of recovery, for with them there is nothing to occupy their attention but food and rest and their own convalescence. Probably most of these are passably healthy birds in autumn, with no sign of having suffered very badly except in their backwardness as regards change of plumage. These birds usually show a great mixture of plumages, having feathers sometimes of the preceding winter plumage, mingled with an irregularly grown nuptial spring plumage and perhaps some new feathers of the already overdue autumn-winter plumage.

The second class is different. They also have a mixture of the same three plumages, but with more complete nuptial feathers, and fewer of the preceding winter plumage. They are the worst of all the sick birds seen in the autumn months. They have been less sick in the spring than the barren birds, but they have been worn out completely by the effort to nest, and by the cares of their family. They have nevertheless won through, thanks to the summer and autumn food supply and summer weather, and by the autumn they are convalescent. By January they will in all probability be once more comparatively strong and healthy, but not so well prepared to meet the critical conditions of early spring as those included in the first class. These, probably, of the second class are the birds that form the first class in the following year, or perhaps they cannot even rise to that, and fall victims to the spring mortality.

CHAPTER VI

THE WEIGHT OF GROUSE

By Edward A. Wilson

THE weight of Grouse in connection with "Grouse Disease" deserves more attention than it has yet received.

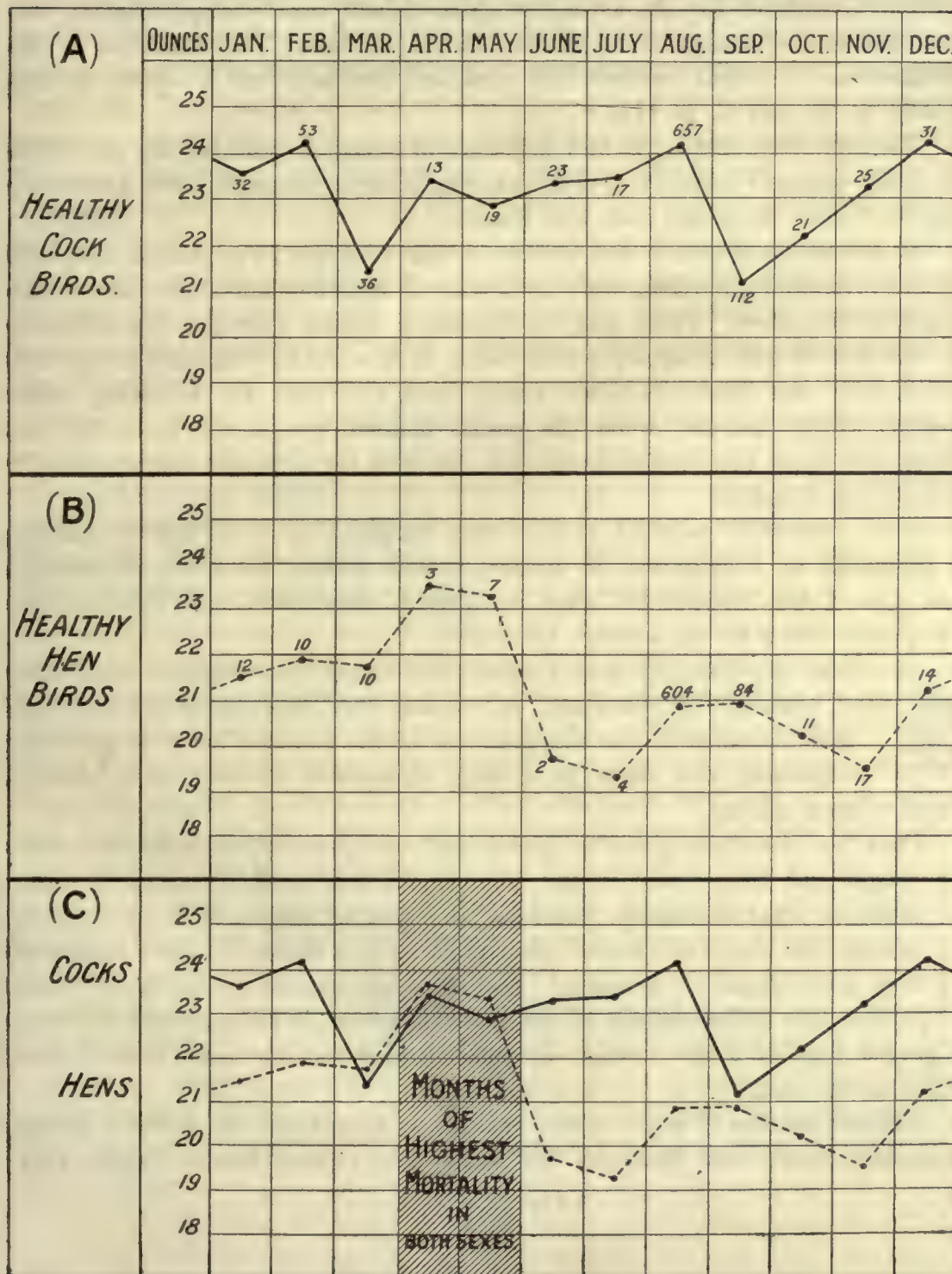
It is a useful indication of the health of a moor, and in the early days of spring a dead bird found and weighed often affords the best rough guide for making a diagnosis of the probable cause of the trouble. Later, when dead birds are found in large numbers, the test becomes convincing if indeed any further proof as to the cause of death is required. Even in November and December a very fair indication of the probability of disease in early spring may be obtained by putting a number of birds upon the scales. A really low average weight in these months is undoubtedly a bad sign, and makes the prognosis for the ensuing year unfavourable; while a good average weight, even if the pigmentation of the plumage is unsatisfactory, need give no cause for alarm.

Apart from its practical value there are sundry points connected with the study of the weight of Grouse in health and in sickness, which are in themselves interesting; and many facts in the life-history of the bird are found upon examination to be correlated with a normal change in weight from one season to another.

It is obvious that before we can usefully investigate changes of weight in sick or dying birds, and can understand their meaning, the seasonal fluctuations of weight in health must be accurately determined and understood.

Beginning, therefore, with healthy Grouse, it is found that sex is a primary factor in determining the weight of an individual bird. An adult cock Grouse is as a rule heavier than an adult hen, when both are well grown and in really good condition. This is true all the year round, except in spring, for at this time when the hen begins to sit she is heavier and in better condition than at any other time

SEASONAL VARIATION IN AVERAGE WEIGHT OF HEALTHY GROUSE.



Note.—The figures at the apices of the curves represent the number of birds weighed each month.

of the year, while the cock is not at his best. There is, therefore, at this season, a tendency for the average weight of both sexes to approximate, and even for the advantage to be on the side of the hen. The difference in the fluctuations of weight between the cock and the hen bird is shown in the Tables A, B, and C, p. 131.

The immediate reason for this difference in spring is probably the one which naturally suggests itself; viz., that the exigencies of courtship have a precisely opposite effect upon the male and female.

In December, the adult cock Grouse's weight averages 24·22 ounces, compared to 21·07 ounces for the hen, while in January it is 23·58 ounces compared to the hen's 21·52 ounces. These may be considered normal averages, the difference at this time of year being dependent wholly upon a sexual difference of size and build, body and bone. In other words, when the birds are all living under healthy conditions, and when the sexual instincts are in abeyance, the hen being less in all her measurements than the cock has a weight correspondingly less by 2 or 3 ounces.

It is, therefore, essential that average weights, to be of use in making a prognosis or a diagnosis of disease, should include the sexes separately; and also if the weights be taken in August, September, and October that every bird taken for an average be adult.

As winter proceeds, we may assume that, unless the weather is unusually open, food becomes less abundant, or, at any rate, less easily obtained and less nutritious; "the sap goes out of the heather," as it is generally expressed, and there is a large proportion of dry, dark, woody, weather-bitten shoots.

Data are elsewhere given to prove that the quantity of such food, both by weight and bulk, found in the crops of full-fed birds in winter, is much in excess of what is usually found in the crops of similar birds in summer. In winter, the crops of Grouse often contain five times as much food-stuff as they ever contain in summer.¹ And, although several factors are at work to produce this difference, one of the most important is the necessity of eating a greater bulk of winter heather in order to arrive at the same total of food value in the end.

Calluna heather is eaten almost exclusively throughout the winter; though Blaeberry stalks and Blaeberry leaf-buds often replace heather, where they

¹ *Vide* chap. iv. p. 79.

are abundant. Heather seed-heads are eaten in preference to the shoots until, in January, the seeds are shed, and then the birds again fall back on the winter heather shoots. It might be expected that the weight of Grouse would suffer from the shortage of nourishment contained in the winter food: but, as a matter of fact, the average weight of both sexes gradually increases during the winter months until March, the worst and most trying month of the whole year for Grouse. February, March, and April must be considered months of greater or less starvation every year, since the winter food has been picked over, not only by the Grouse themselves, but by cattle, sheep, deer, and hares, and often, too, the whole moor has long been buried deep in snow, or the heather has suffered badly from frost or from the dry parching effect of north-east winds. Sometimes the roots have been frozen in the surface soil, and the soil has been too cold to allow even a drain of sap to rise, so that the Grouse are hard set to find food enough to maintain their weight. Although the hen appears able to remain in good condition, the cock always loses weight to some extent at this time—often far too much—and in consequence suffers from a diminished power of resistance to Entozoa. When thus half-starved, and long before he has any chance of recuperation, the exhausting necessities of courtship force themselves upon him.

The cock bird in February is still in full winter plumage, and by March, though he possesses well-developed supraorbital combs, these alone of all his attractions can be considered a special addition to his winter dress for courtship. These crests or combs over the eyes are erectile organs of a brilliant crimson colour, and inconspicuous or even invisible as they are when the bird is at rest, they become in excitement so erect and tense as almost to meet above the top of the head. They are then visible from afar, and are indications of the nervous tension of the breeding season. The bird is at this time bold, noisy, aggressive, jealous, excitable, pugnacious, and magnificent to see. He struts, becks, flies constantly about from one hillock to another, defies all comers, fights viciously, eats little, and constantly attends his mate.

Throughout February and March he leads this exhilarated but exhausting and unsettled life, constantly at war, and daily becoming more and more reduced in weight. In addition to all this, he is probably loaded up with parasites, and, though he may live to recover, the strain is often too great, with the result that it is in April and May that the majority of cock birds die of disease.

With the hen, however, it is very different, for at this time she leads an even quieter life than usual. She feeds constantly, takes no part in the warfare of her mate, and becomes to a greater or less extent "broody." When in this condition she does not readily take the wing, and puts on flesh and fat. By the time she begins to lay she has a very large store of surplus fat deposited throughout the body and in masses under the skin; and from this reserve she draws during the three weeks of incubation. For the twenty - three days during which she "sits" she leaves the nest only for a few minutes night and morning, to eat and drink, and her tracks and "clocker" droppings are to be found always at the springs or drinking-places, which happen to be nearest to her nest.

Hen in
breeding
season.

At the beginning of the nesting season the hen Grouse weighs as much as a heavy cock, sometimes even up to 27 ounces; but this holds good for a short time only. It is just during these two months of the year, April and May, that she suffers most from "Grouse Disease"; an inexplicable fact, did we not know that for various reasons, which are given below, March is to be considered the most dangerous month of the whole year for infection with *Strongylosis*.

As the hen sits, her weight, even in health, rapidly diminishes. She is living largely upon her reserve material, and has, in addition to produce from eight to ten eggs. This must be a very considerable drain upon her system, since each egg weighs about an ounce, and each ounce so lost to her is an ounce of her "flesh and blood," the whole amounting sometimes to nearly half her eventual total weight. By the end of June, thanks also to the trials of a family, she reaches an average weight of less than 20 ounces, and by the end of July sometimes falls to 19·5 ounces, whereas the cock, benefiting daily by the improving food and weather, gradually rises from 19 or 20 ounces in March to an average of 24 ounces in August.¹

It will perhaps throw light on the cause of the marked changes which appear in Tables A and B if an attempt is made to account for them month by month.

In Table A, for example, which gives the monthly averages for the healthy male Grouse, there is a very decided fall from 24·2 ounces in February to 21·45 in March, with a gradual rise again from April to August.

This sudden drop must be due to courtship, rather than to shortage of food, for though food is scarce at this time the shortage makes no difference

¹ *Vide* p. 145, note.

worth noticing in the case of the hens (*see* Table B). This argument is borne out by the almost equally sudden rise as soon as the mating is over.

The post-nuptial moult in the male takes place in April and May. It is complete in June, therefore any loss of weight in the replacing of new feathers would make itself felt in the earlier of these three months. From April to August the food supply is improving daily, and the weight of the cock Grouse gradually increases. And it is by no means easy to see why there should be a sudden drop in September unless it is due to the complete (male) moult to the winter plumage. As there is no corresponding drop in the hen, and, as we know, no similar moult, we are probably right in thus attributing for the September fall in the weight of the male to this autumn moult.¹

It is, however, true that although healthy Grouse are at a much lower ebb, as evidenced by their average weight, during certain months of the year than during others, Strongylosis does not necessarily kill them off at these seasons. It kills off the hens when they ought to be at their flood tide of health and vitality; and the cocks when they ought to be on a good rising average tide.

We have thus a paradox which may be stated in the following way:—

More hens die of Strongylosis during April and May than in any other month of the year, notwithstanding the fact that the healthy hen is then at her best so far as weight, fat, and plumage go.

More cocks die of Strongylosis during April and May than in any other month of the year, notwithstanding that the healthy cock is then already recovering the weight which he lost during courtship, and is at a fair average and rising weight.

And although one might expect cock birds to die in March and September, when the average weight is at its lowest, this does not occur.

And whereas one might expect hen birds to die in June and July, or in November, when the average weight in health is at its lowest, this also does not occur.

In attempting to explain this paradox, it is necessary to recapitulate shortly the conditions which lead to an over-infection of the Grouse with the young *Trichostrongylus*.

Elsewhere it has been pointed out that, owing to the small proportion of

¹ The cock Grouse normally moults twice a year, first between April and June, and secondly between August and November. The normal hen Grouse also moults twice a year, first between February and April, and secondly during July and August.

heather which produces good food during the months of February, March, and April, all the birds upon a moor are forced to concentrate upon small areas of feeding ground.¹ Consequently, there is a tendency for these small areas to become heavily infected with the *Trichostrongylus* even from the droppings of healthy birds. At first there are no evil results, for the eggs take some weeks to go through the necessary stages of metamorphosis before the worms become actively dangerous to the health of the bird.² Thus, even by the end of February and beginning of March, there is comparatively little mortality among Grouse.³ As time goes on, however, the infection becomes more and more intensified, for not only do the larval nematodes assume their most active form, but those which have been eaten by the Grouse at the beginning of the period have had time to grow up and produce eggs in the intestine of their host, and these eggs are in turn distributed over the moor to add to the moor infection. The unhealthy conditions do not result in immediate mortality—it has been shown by experiment that birds which have been fatally infected may not die for many weeks.⁴ In some cases a severe infestation does not result in death.⁵ Even in March the mortality has not reached its height,⁶ for the majority of birds fatally infected in March will probably not die till April. The infection of the ground continues to increase, and if the same conditions were prolonged for another month or two it is possible that on the majority of moors hardly a bird would survive. Fortunately the advent of spring brings a blessed relief to the plague-stricken stock, and with the first appearance of new heather growth at the end of April and beginning of May risk of fresh infection is past.

Thus it is that in April the infection reaches its climax, but the birds which die in April are probably the result of infection in March, whereas the birds infected in April die in May, even although the conditions have improved.

This is the explanation of the paradox stated on p. 135.

It may be assumed that both cocks and hens have the same opportunities for obtaining food, and that the quantity and quality of that food is the same for each, consequently each will be equally liable to infection by the Strongyle worm. Why then do the cocks die in larger numbers than the hens? Only one answer is possible, and that is, that whereas at this time the power of resistance of the cock is at its lowest, the power of resist-

¹ *Vide* chap. iv. p. 81.

⁴ *Vide*, vol. ii. Appendix F.

³ *Vide* chap. x. p. 224.

⁵ *Ibid.*

² *Vide* Chart F, p. 142.

⁶ *Vide* Chart F, p. 142.

ance of the hen is at its highest. The fact is sufficiently proved by the comparison of the weights of the sexes, but if further confirmation be required it would be found in the fact that in June as the cock increases in weight so he becomes less liable to disease, whereas the hen, whose weight is on the downward grade, continues to suffer, and sometimes to die, throughout the summer months.

The fact that the average weight of the cock is slightly on the upward grade during the months of greatest mortality is somewhat misleading, unless it be remembered that he is still far below his best condition, and was probably about his worst at the time when he first contracted the infection.

The reason why cocks do not die in September, or hens in November, when their respective weights are again at their lowest, is obvious—mere loss of condition is not enough to cause death. It is only where this loss of condition is found in conjunction with a heavy infection of parasites that it becomes a source of serious danger.

To return, however, once more to the healthy bird, it is to be remembered that in June the hen undergoes a complete post-nuptial moult, changing from the now faded breeding or nuptial dress, to the autumn or summer plumage, and this she cannot do without an appreciable drain upon her resources.

In changing the winter plumage for a nuptial breeding dress in January she differs radically from the cock, who retains his winter plumage until the breeding season is over. The two sexes moult at different seasons, and each twice within the year. The details of the changes have been carefully investigated and described by Mr Ogilvie-Grant, and have been dealt with in another chapter of this Report.¹

It has been pointed out that the cock bird begins to grow new feather in March and in August; whereas the hen bird begins to grow new feather in February and July; and each of these moults appears to have a definite effect upon the weight of the bird. There are, therefore, ^{Effects of} ~~moult.~~ fluctuations in the weight of the healthy Grouse, which are partly due to the moult, and are therefore seasonal, while others are purely sexual; it must be noted that the seasonal fluctuations differ as to date in each sex. Both seasonal and sexual changes occur in normal healthy birds. These fluctuations must be fully recognised before any useful deductions can be drawn regarding the changes of weight in birds that are or have been diseased.

¹ See chap. iii. p. 34.

The effect of the various influences which affect the weight of the healthy Grouse are shown in Tables A, B, and C.¹

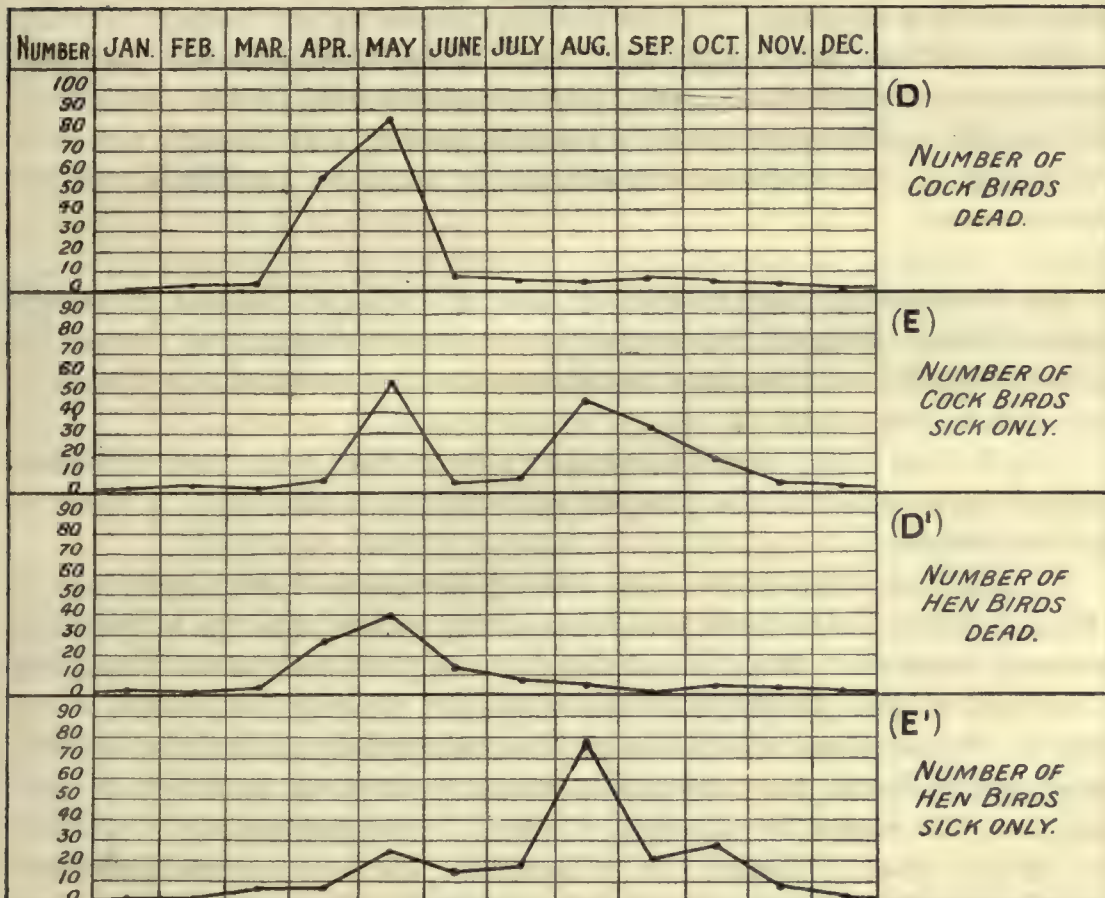
It is unfortunate that some of the monthly averages have been taken from such a limited number of birds. This, in the breeding season, is unavoidable. There is a very natural objection to the wholesale destruction of healthy sitting hens for any purpose. Even dead birds are less likely to be found at this time of year than at any other, for the reason that the majority of gamekeepers dislike the disturbance of their moor which is entailed by a systematic search.

It is partly to this feeling amongst keepers that one should attribute the prevalence of the belief that "Grouse Disease" mortality is confined to the spring and autumn with a break between. There is no doubt that the least observed and least understood portion of the life cycle of a Grouse moor is that which lies between May—when the early broods are hatched off—and the end of July, when the dogs are taken out to make a survey of the shooting prospects. Conversely, too, from the intimate knowledge of the moor after August 12th, undue importance has been attached to the idea of autumn disease owing to a certain number of sickly birds being found in the August and September bags—birds which would otherwise have escaped notice altogether, but which were shot in the day's sport, and afterwards picked out as "piners." The point is clearly shown by Charts D, E, D¹, E¹, p. 139.

It is by no means a rare thing to find hens weighing 14 and 15 ounces still capable of flight. Often such birds are shot and afterwards picked out of the bag as "piners" to be examined, and condemned as cases of disease.

The appearances of ill-health are generally abundant. To begin with, the bird is undersized, the bones are found to be unusually small in their measurements and slight in their structure, suggesting that the bird was bred late in the previous year. This gives it a bad beginning, and means that the bird, lacking strength, suffered more than the early bred birds during the previous winter months. If the bird is a hen, it will be evident from the naked skin of the abdomen, from the delayed moult of the feathers of the upper parts, and from the almost featherless condition of the legs and feet, that a long and exhausting period of incubation has been endured, followed by a period of incessant watchfulness while the young brood required protection. Often enough a hen "piner" in this condition appears to have suffered from no more definite

CHARTS SHEWING THE FALLACY OF THE AUTUMN OUTBREAK OF DISEASE.



disease than this over-sitting. This in a weakly hen is in itself a sufficient cause of extreme emaciation.

Then, again, it may be found that the bird is replete with parasites. These, if the case is a true "piner," will be abundant within and without. The feathers are often alive with *Nirmus* and *Goniodes*, the small flat Bird Lice, and the head of the bird is dotted, especially round the eyes and ears, with Ticks of the genus *Ixodes*. The presence of *Ornithomyia*, the Grouse fly, depends more upon the weather and season than on the condition of the host. Within, the duodenum will be occupied by a mass of *Hymenolepis* (tapeworms), or *Trichosoma* (threadworms), or both; the main gut by a far more bulky mass of *Davainea* (tapeworms); and the cæca may be reddened from end to end by

villous engorgement due to the irritating presence of thousands of *Trichostrongylus* (threadworms). In this state the bird is flushed and shot, and forwarded for a diagnosis.

And still one more perplexing item, namely, that scattered here and there amidst a hundred thousand *Trichostrongylus* ova, in the contents of the intestine, are encysted spores of *Coccidia*, showing that the bird may have lost weight in the height of the summer by excessive Coccidiosis, and yet have survived.

Our investigations have established that one form of sickness commonly called "Grouse Disease" is due to the excessive infestation of Grouse by *Trichostrongylus*, and the most easily recognised symptom of this disease is loss of flesh and weight.

It is for this reason that the average weight of birds is the best indication that can be obtained of the prospect of health or disease upon a moor in the near future.

The tradition, for it is probably nothing more, that in some outbreaks of "Grouse Disease" birds have been found dying or dead well up to weight is discussed elsewhere.¹ Birds do not die of Strongylosis without exhibiting loss of flesh and weight. Neither do Grouse chicks die of Coccidiosis without losing weight. Beyond these two diseases we have no knowledge of any other disorder which attacks Grouse over considerable areas of country, and kills them in large numbers. The reason for this loss of weight in Strongylosis and Coccidiosis can be seen when a diseased bird is dissected. The *post-mortem* appearances are fully described in other parts of this Report.²

Conditions affecting the weight of Grouse. The following list includes most of the conditions which commonly affect the weight of Grouse:—

I. IN HEALTH.

- (a) *Sex*, generally in favour of the male, but in April and May rather to the advantage of the female.
- (b) *Late hatching*, producing birds of both sexes unready for the winter; birds which have missed the best growing months of summer, and which therefore remain permanently undersized and of a poor physique though not actually diseased.

¹ *Vide* chap. ix. pp. 204 *et seq.*

² *Vide* chap. xii. p. 288; chap. xi. pp. 257 *et seq.*

- (c) *Moult*, in the male taking most effect in March and in September; in the female in July and November; probably always leads to some loss of weight in either sex.
- (d) *Courtship*, in the male always apparently a cause of loss of weight: in the female, owing to increased rest, with some change in the general metabolism and extra opportunities for feeding prior to incubation, seems to lead normally to a very considerable increase of weight.
- (e) *Egg laying and incubation*, gradually lead to a loss of weight, which becomes more marked when the hen has had the care of a family of chicks. These cares, notwithstanding the abundance of summer food, often result in producing the lowest possible weights in hens, such loss of weight being in some cases due to an attempt to rear a second brood.

During the hen's incubation the cock somewhat recovers his weight, possibly because the food supply is rapidly improving, and because his energies are not so exhausted by courtship.

- (f) *A shortage of good food* in a bad winter must often be responsible for a great reduction of weight, and indirectly for an increase of the mortality in both sexes due to *Strongylosis* in the spring. Similarly the abundance of food in summer, autumn, and early winter must serve to counteract some of the other causes of loss of weight.

II. IN DISEASE.

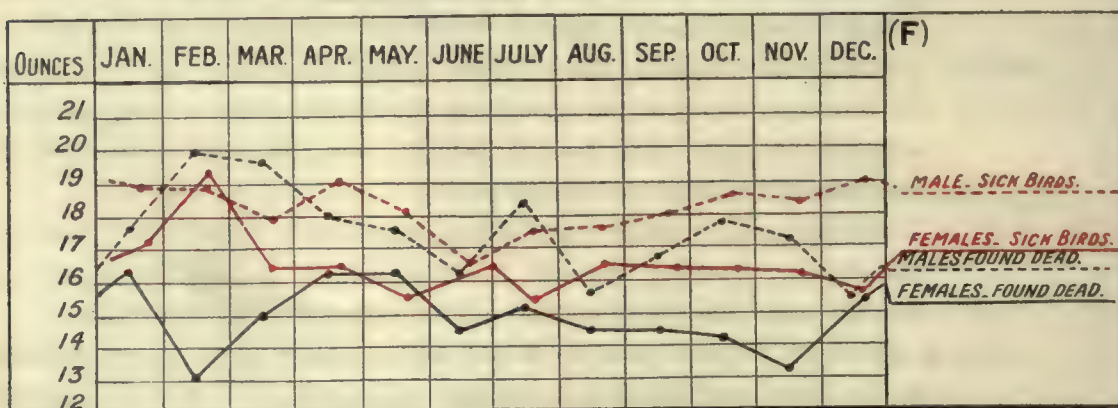
- (a) *Strongylosis* in both sexes and at all ages leads to excessive loss of weight, and ultimately to death, but the maximum incidence of infection is strictly seasonal, accounting wholly for the fact that both sexes die in April and May in very much greater numbers than in any other months of the year. The observation that so many more cocks die than hens has been explained largely by the fact that the average power of resistance of the normal hen Grouse is at its best in April and in May; while that of the normal cock has just been at its worst.

Another factor which bears on this question is shown by reference to Chart F, p. 142, which shows the average monthly weight of cocks and hens found sick but alive and found dead of *Strongylosis*

respectively. This table has been prepared to illustrate that birds found sick show the same tendency to lose weight though they do not record such a marked loss as those which have actually succumbed to disease.

CHART F

COMPARISON OF AVERAGE WEIGHT OF SICK BIRDS AND OF BIRDS FOUND DEAD; BOTH OF STRONGYLOSIS.



The curve shows that birds succumb at very different stages of emaciation, in different months of the years. For example, in the case of the cocks a bird will die at 20 ounces in February, at 19 ounces in March, at 18 ounces in April, at 17 ounces in May, and at 16 ounces in June—the conditions of weather and food making life easier month by month as warmth, sunshine, and increasing abundance of food enable the sick bird to cling to life a little longer.

It is interesting too to note that in the case of the hens, although the average weight in health is 23 to 24 ounces in April and May, it falls in fatal disease to 16 ounces, whereas the cock bird, whose average weight in health is also 23 to 24 ounces for the same two months, succumbs at 17.5 to 18 ounces.

- (b) *General Helminthiasis*, including all disorders due to worms in birds of both sexes and at all ages must also have a share in causing loss of weight: (1) by disturbing the normal digestion and

assimilation; (2) by the production of toxins in the alimentary canal, many of which are absorbed by the blood; and (3) by (but this is a minor matter) the worms absorbing, living on and growing on food which in their absence would have served to nourish their host.

- (c) *Coccidiosis*, especially in young birds, causes excessive emaciation and frequently death.¹

It would be interesting, were it possible to collect sufficient figures, to compare local variation in the average weight of healthy males or females with local differences in the height above sea-level, the rainfall, the character of the subsoil, or the prevalence of disease. For this purpose it would be reasonable to take wide natural divisions such as those which are plotted out for meteorological records, in preference to artificial divisions such as county boundaries and political districts. In attempting this, however, it must be remembered that for a number of years it has been the practice to introduce birds from one part of the country to another, perhaps a hundred miles or more away. This practice makes it difficult to trace true local variations either in size or in other characteristics. It is true that particular districts have been credited with the production of birds distinctly above the average in size and weight. Midlothian, Caithness, and the west coast of Scotland each claim to produce Grouse of a high average weight.

To establish this a much more extensive series of weights should be taken than has hitherto been possible. So far as the Committee have been able to ascertain, it is difficult to say with certainty that any one district produces birds of a definitely larger type than any other. The result of the evidence collected is given in the form of a Table on p. 144.

¹ *Vide* chap. xi. pp. 252 *et seq.*

[TABLE.

THE GROUSE IN HEALTH AND IN DISEASE

TABLE SHOWING AVERAGE WEIGHT OF GROUSE FROM DIFFERENT DISTRICTS.

County.	Date.	Cocks.					Hens.				
		Number of Birds Weighed.	Gross Weight.	Average Weight.	Heaviest Bird.	Lightest Bird.	Number of Birds Weighed.	Gross Weight.	Average Weight.	Heaviest Bird.	Lightest Bird.
			lbs. ozs.	ozs.	ozs.	ozs.		lbs. ozs.	ozs.	ozs.	ozs.
SCOTLAND—											
1. Caithness	Various	14	20 10	23·6
2. Sutherland, No. 1 Moor	Aug. 24	12	19 1	25·4	12	16 0	21·3
" " 2 "	" 24	12	18 0	24	12	15 6	20·5
" " 3 "	" 24	20	29 8	23·6	20	26 0	20·8
" " 4 "	" 30	20	31 0	24·8	20	30 0	24
" " 5 "	" 24	12	18 0	24	12	16 0	21·3
" " 6 "	" 24	20	27 10	22·1	20	24 8	19·6
" " 7 "	" 23	12	17 13	23·7	12	15 6	20·5
" " 8 "	" 26	20	30 3	24·1	20	26 2	20·9
" " 9 "	" 22	12	18 3	24·25	12	16 13	22·4
" " 10 "	" 26	12	18 0	24	12	15 0	20
" " 11 "	" ...	12	17 5	23·1	12	15 10	20·8
" " 12 "	" 23	10	14 5	22·9	10	13 7	21·5
Average for County . .		174	259 0	23·9	174	230 4	21
3. Ross-shire, No. 1 Moor	" 16	3	4 8	24	2	2 12	22
" " 2 "	" ...	12	19 0	25·3	12	16 0	21·3
Average for County . .		15	23 8	25	14	18 12	21·4
4. Inverness	98	148 2	24·35
4a. Skye	Aug. 24	1	23 0	23
5. Moray	4	5 13	23·37
6. Banffshire	" 16	10	15 1	24·1	10	12 14	20·6
7. Aberdeen, No. 1 Moor	...	12	19 8	26	12	16 5	21·7
" " 2 "	...	12	18 0	24	12	16 0	21·3
" " 3 "	...	12	18 9½	24·7	12	15 13½	21·1
" " 4 "	...	12	20 2	26 8	12	16 4	21·6
Average for County . .		48	76 3½	25	48	64 6½	21·4
8. Kincardine	" 12-14	32	...	23·23	25	...	19·9
9. Forfar	12	19 0	25·3	12	16 0	21·3
10. Perthshire	" 14	17	...	23·4	28	19	10	...	20·2	22	19
" " " " " "	" 16	18	...	23·5	24	23	9	...	20	24	16
" " " " " "	" 19	16	...	23	26	18	10	...	20	24	18
" " " " " "	" 20	4	...	23	24	21	3	...	18·6	20	17
" " " " " "	" 22	8	...	24·4	26	23	2	...	20	21	19
" " " " " "	" 24	7	...	23	23	23	8	...	20·5	24	18
" " " " " "	" 27	8	...	24·6	27	23	4	...	22	23	20
Average for County . .		73	...	23·5	46	...	20·2
11. Stirlingshire	" 14	1	1 8	24
" " " " " "	" 21	1	1 4	20
" " " " " "	" 31	12	18 10	24·8	28	23	8	11 0	22	23	21
" " " " " "	Sept. 28	4	6 2	24·5	25	23	4	4 15	19·7	22	18
" " " " " "	Nov. 18	9	12 2	21·5	26	18	10	12 1	19·3	22	17
" " " " " "	Dec. 7	7	10 5	23·5	26	21	8	10 5	20·6	24	18
Average for County . .		33	48 11	23·6	31	39 9	20·4

General average weight of full-grown Grouse at commencement of shooting season :—Cocks, 23·97 oz. ; hens, 20·65 oz.

THE WEIGHT OF GROUSE

145

TABLE SHOWING AVERAGE WEIGHT OF GROUSE FROM DIFFERENT DISTRICTS.—*continued.*

County.	Date	Cocks.					Hens.				
		Number of Birds Weighed.	Gross Weight.	Average Weight.	Heaviest Bird.	Lightest Bird.	Number of Birds Weighed.	Gross Weight.	Average Weight.	Heaviest Bird.	Lightest Bird.
SCOTLAND—											
12. Argyllshire	Aug. 12	13	...	23·7	14	...	20·5
" " " " "	" 13	12	...	24	11	...	20·4
" " " " "	" 15	5	...	24·4	6	...	21·3
" " " " "	" 16	10	...	24·2	27·5	...	3	...	22	23	...
" " " " "	" 20-24	12	...	24·5	12	...	21·25
" " " " "	" 20-24	12	...	25·5	12	...	22·5
" " " " "	" 14	12	18 0	24
Average for County . .		76	18 0	24·3	27·5	...	58	...	21·3	23	...
12a. Mull	Aug. 16	1	25 0	25
13. Fife	43	62 8	23·27
14. (Dumbarton)	" 12-20	12	...	23	12	...	21
15. Midlothian	5	7 4	23·25
16. Haddington	14	20 12	23·78
17. Arran	5	7 10	24·45
18. Ayrshire	10	...	24	10	...	20
19. Lanark	1	1 9	25
20. Berwickshire	" 19	12	18 0	24	12	16 0	21·3
21. Dumfries	8	10 6	20·78
22. Roxburgh	3	4 8	24·33
23. Peebles	30
24. Selkirk	24·6	26·5	21·2	23·5	...
25. Kirkcudbright	1	...	21
26. Wigtown	1	...	24
ENGLAND—											
27. Northumberland . . .	Sept. 10	12	18 15	25·25	12	15 12	21
28. Durham	5	8 0	25·6	4	5 0	20
29. Cumberland	1868, Sept. 17	28·5
" " " " "	1873, " 5	28·5
Average for County	28·5
30. Westmorland	10	14 5	22·97
31. Yorkshire	Aug. 12	10	15 8	24·8	10	14 8	23·2
" " " " "	" 12	10	15 7	24·7	10	13 4	21·2
" " " " "	" 23	10	14 11	23·5	10	13 12	22
" " " " "	" About Aug. 17	20	29 8	23·6	20	25 8	20·4
" " " " "	" Aug. 23	12	18 6	24·5	12	16 1	21·4
Average for County . .		52	93 8	24·2	62	83 1	21·5
32. Derby	" 13	15	28 0	24·5	15	20 0	21·3
WALES—											
33. " " " " "	" 13	20	29 10	23·7	27	22	20	26 9	21·25	24	19
IRELAND—											
34. Donegal	1	25 8	25·50

General average weight of full-grown Grouse at commencement of shooting season:—Cocks, 23·97 oz.; hens, 20·65 oz.

The heaviest cock Grouse which came before the notice of the Committee was one of exactly 30 ounces from Peebles.

Macdonald, in "Grouse Disease,"¹ says : "The Grouse in Scotland is a larger and finer bird than that met with in England," a remark which the above figures do not altogether uphold.

Macpherson, in Fur and Feather Series, says : "The cock birds not infrequently weigh 28 or 28½ ounces in the north of England, when in first-rate condition in every respect. Anything over 30 ounces is noteworthy, but a weight of 32 ounces is not unprecedented."²

In Yarrell's "British Birds,"³ Red Grouse are said to be at their best, both as regards weight and plumage, in November; but this is only partly true. Their best months are February, August, and December; and one may say they are at a fair level of condition in those months.

¹ Macdonald, "Grouse Disease," p. 103.

² Fur and Feather Series, "The Grouse," p. 64.

³ Yarrell, "British Birds," vol. iii. p. 77 (edited by Howard Saunders). Fourth Edition. London : John Van Voorst, 1882-1884.

PART II.—THE GROUSE IN DISEASE

CHAPTER VII

CAUSES OF MORTALITY IN THE RED GROUSE

By Lord Lovat and Edward A. Wilson

IN classifying all diseases it must be remembered that before it can be scientifically named it is necessary to ascertain whether the disease in question has an individuality which can be specifically described and recognised by definite characteristics and symptoms.

Rules for
the study
of disease.

It is an accepted rule of medical science that the primary cause of a disease must be found before any attempt can be reasonably made to discover a cure. Yet this important rule has been almost wholly ignored by the majority of writers upon "Grouse Disease," with a few notable exceptions, such as Klein, Cobbold, and Farquharson.

Ascertain-
ment of
primary
cause.

Hardly a writer on the subject but dwells in vague generalities, hopelessly mixing up observed facts with unsound theories, and primary with predisposing causes; for instance, if the chief object of the writer of the following paragraphs had been to confound an already almost hopeless confusion, he could hardly have been more successful:

Fault of
previous
observers.

"What I still maintain is that the unwholesome food which Grouse have been compelled to eat has occasioned both the worms with which they have been infested and at least one type of the disease."

"The disease appeared in all its virulence after the heather had been damaged by hard frost; but the crying evil is undoubtedly the overstocking of the moors with sheep."

"Grouse have materially suffered from cold late springs which have blighted the heather."

"Granting as I do that this nasty little parasite *Strongylus* does occasion disease in Grouse, is there anything illogical in attributing the cause of the

worm to the bird being compelled to eat unwholesome food, from its natural food the heather being damaged or destroyed from continued blighting east wind? And thus the blight of the heather is really at least one cause of 'Grouse Disease.'"

"Insufficient or unwholesome food is the cause at least of one type of disease amongst Grouse."

Or the following:—

"'Grouse Disease' is caused mainly by overstocking, over-preservation, and the complete and indiscriminate slaughter of certain species of so-called vermin, notably the Peregrine Falcon; also by the state of the young and old heather after severe and late frosts which do much more harm now that heather burning is done systematically. Also by greed for big stock. Unnatural and rapid burning of heather and a wholly artificial state of Grouse farming; also interbreeding."

In the above quotations, which are perfectly sound so far as they go, we have a very fair summary of possible predisposing causes; but the immediate cause of "Grouse Disease," whether we consider the disease to be pneumonia, or Strongylosis, or Coccidiosis, or Enteritis, or any other sickness in the world, is not touched.

The primary or acting cause of Klein's acute infectious pneumonia was believed to be a sub-species of the *Bacillus coli*; the primary cause of Cobbold's Strongylosis is the nematode worm *Trichostrongylus pergracilis*; the primary cause of Grouse Coccidiosis is *Eimeria (coccidium) avium*, and so on; not east winds or the absence of the Peregrine Falcon.

Until we have discovered the active agent in a disease we cannot say that we know its cause. This is a fundamental rule, and to be satisfied with predisposing causes is to be satisfied with less than half the truth, though that half is, of course, very important if our intention is to proceed further in the attempt to discover a remedy for the disease in question.

The consequences of what has appeared to be epidemic disease amongst Grouse have been so disastrous from time to time in the past that it is not surprising to find a very widespread tendency amongst sportsmen and gamekeepers to attribute every death and every case of sickness on the moor to the so-called "Grouse Disease."

All mortality in Grouse ascribed to "Grouse Disease."

It is obvious that Red Grouse, in common with other birds, may be subject to more than one form of disease; but when a certain form of

sickness takes an undisputed pre-eminence above all others for a century, as has been the case, apparently, with the Red Grouse sickness, there is some justification for the use of such an expression as "The Grouse Disease," and some excuse for the view held, by those who cannot go into the minutiae of microscopic work or of dissection, to ascribe all mortality on a moor to this one disorder.

It has been the object of the "Grouse Disease" Committee to investigate this question, and to find out amongst other things:—

(1) Whether the sickness described universally as "The Grouse Disease" in all the literature of the past century which deals with the subject is, in truth, a single disease with individual character peculiar to it alone? (2) Whether a distinction can be discovered between various recorded outbreaks of the so-called "Grouse Disease" which will justify the opinion held by many writers that two distinct forms of disease, due to two distinctive causes, are confused under the one term? (3) In the event of a finding in favour of the belief in two or more distinct epidemic diseases, what are their respective causes and effects, and by what distinctive titles and characteristics should they be known? (4) In the other event of a finding in favour of the belief that only one epidemic disease exists, is Professor Klein's view right, that the only serious disorder amongst Grouse, to which all past records of disease refer, is the one which has for its cause a *Bacillus* of the *B. coli* group, and for its chief morbid characteristics the lesions of an acute pneumonia in the lung, and "all the characters of an acute infectious epidemic disease"? Or, (5) is Dr Cobbold's view right, that there is a pseudo-epidemic disorder amongst Grouse, answerable for all the recorded outbreaks of disease, which has for its cause a nematode worm of the genus *Trichostrongylus*, and for its chief morbid characteristics certain lesions in the cæca due to chronic irritation, leading to extreme emaciation? (6) Is there any other form of "Grouse Disease" which is the cause of extensive mortality, but which has hitherto been overlooked?

The objects
of the
Inquiry.

These are questions which have to be answered before it can be said that we understand the forms of "Grouse Disease" sufficiently to classify them systematically. With a view to defining the main divisions under which the next five chapters are arranged, it may be well at this stage to give in anticipation a brief summary of the conclusions at which the Committee has arrived.

Results of
Com-
mittee's
investiga-
tion.

The Committee is of opinion :—(1) That the sickness which has in the past caused "Grouse Disease" among the great majority of adult birds is a single disease with clearly defined characteristics of its own ; (2) and (3) it follows that if the two forms of "Grouse Disease" hitherto described as distinct diseases are, in fact, one and the same disease, there is no longer any need to differentiate between them ; (4) that "Grouse Disease" is not due to an acute infectious pneumonia caused by the presence in the lung of Klein's Bacillus ; (5) that adult "Grouse Disease" is caused by the presence of Cobbold's *Trichostrongylus* in large numbers in the cæca ; (6) that another form of disease in Grouse exists which has hitherto escaped notice. This disease is caused by the presence of *Eimeria* (*Coccidium*) *avium* in the alimentary tract, and is referred to in the Report by the name of "Coccidiosis." It is improbable that Coccidiosis can have been responsible for any of the outbreaks of so-called "Grouse Disease" in the past, for, so far as the Committee's experience extends, it is only the chicks that succumb to this disease, whereas the records of "Grouse Disease" refer only to mortality among adult birds.

The grounds on which the foregoing conclusions are based form the subject of chapter ix. ; chapter x. is devoted to a description of the *Trichostrongylus pergracilis* of Cobbold, the primary cause of "Grouse Disease" proper, and chapter xi. deals with the *Coccidium avium* and Coccidiosis in relation to young Grouse.

We have still to discuss the less important diseases of Grouse, of which quite a considerable list may be given ; though their interest is greater from a purely academic point of view than as a serious menace to the well-being of a moor : indeed with one or two possible exceptions, there is not much probability that they will ever give cause for much anxiety. The exceptions occur most commonly in consequence of the proximity of Grouse moors in certain districts to low-ground shootings heavily stocked with Pheasants and Partridges. It is well known that these latter birds are often the victims of various forms of Enteritis, and cases have been reported to the Committee of Grouse dying of disease apparently contracted from Pheasants which have strayed on to the moor.

Amongst other causes of death may be mentioned diseases connected with the reproductive functions, diseases connected with the seasonal moults and diseases caused by deficient or unwholesome diet.

But apart altogether from mortality due to disease, a large number of

deaths are directly or indirectly due to accident or to artificial causes. Many of these causes may be traced to the agency of man, and it will be shown elsewhere to how great an extent some of them are avoidable by attention to the details of moor management. Other causes of mortality.

Shooting, in all its forms, is responsible for a great deal of unrecorded damage amongst Grouse; and the examples of "pricked" birds which have come to the Committee's notice, generally sent as "diseased" birds for examination, show amongst other things how extraordinarily active is the recuperative power of an animal in a state of nature. Bones are fractured and reunited, even those of the wing, allowing the bird to survive, to be shot again the following year.

Peritoneal adhesions may shut off a perforation of the intestine, and even result in a short-circuit of the gut before leakage has caused sufficient general peritonitis to result in death.

Chapter viii. deals with the mortality and damage due to accidental causes, or to natural causes other than true "Grouse Disease," and thus clears the way for the proper consideration of the main subject of the investigation, viz., death due to "Grouse Disease."

CHAPTER VIII

CAUSES OF MORTALITY IN THE RED GROUSE—*continued*

By Edward A. Wilson

THE causes of death and damage to Grouse not due to "Grouse Disease" may be classified as follows:—

A.—THOSE REFERABLE TO ARTIFICIAL CONDITIONS.

Accidental consequences of sport, wire-fencing, telegraph-wires, sheep-drains, vermin-traps, poison, etc.

B.—THOSE REFERABLE TO ^{Natural}~~ARTIFICIAL~~ CONDITIONS.

Extremes of climate ; cold, heat, wet, snow, etc.

Destruction by birds and beasts of prey, so-called "vermin," and by the pugnacity of the Capercaillie and Blackgame.

Exigencies of reproduction : fighting of cocks, over-sitting of hens, egg-binding, gastro-uterine, gestation, etc.

Exhaustion due to moult, and to skin disease affecting the growth of feathers.

Deficient diet and starvation, due to frosted, blighted, and over-age heather or to heather-pests ; deficiencies of grit and water ; excessive or injudicious burning ; and feeding on unwholesome foods, *e.g.*, corn-stooks and sour grain.

A.—Causes of Death and Damage resulting from Artificial Conditions.

Under this heading there are some causes which may be passed with a mere mention.

Death and
damage
from arti-
ficial
causes.

One might do so with all, perhaps, were it not for the interest attaching to some of the cases which have come before the Committee, and the light which they throw on the recuperative power

of birds in the wild state. Some of these cases occurred in birds which had died naturally; in others the specimen had been shot, and forwarded for examination as a possible case of disease.

The following accidents are within the experience of most game preservers: collision with wire fences and telegraph wires, accidental damage from vermin traps, snapping by sheep dogs, drowning in sheep-drains or moss-cuttings, etc., and wounding by shot.

And of these no one can doubt that the "pricking" of birds due to bad shooting is the most frequent cause of damage.

The following examples illustrate a number of these points:—

(No. 301.) A hen Grouse whose wing had been cut off clean at the shoulder, presumably by collision with a wire fence, not only survived to be shot the following season under suspicion of being a sick bird, but actually succeeded in rearing a brood of five healthy young Grouse. Collision with wire.

Another instance of precisely similar nature is recorded elsewhere, in which the bird, a hen Grouse, had successfully raised a brood of healthy chicks notwithstanding the loss of a wing. In the first of these cases the wing was cut off so close to the body that no vestige of a stump was left. The cicatrix in the skin was adherent to the tissues about the rounded end of the broken humerus, of which only the head and neck were left. There was every appearance that the wound had healed well and quickly, probably some four or five weeks before the bird was shot, and soon after the nesting time. In feather and in condition the bird was not appreciably the worse for her mishap. The scapula, which had been broken in two pieces at the time of the accident, had made a strong though irregular union (*see* Fig. 1). For purposes of comparison a drawing is given of the bones of the undamaged (right) side of the same bird (*see* Fig. 2).

The sternum or breastbone is another bony part also liable to injury, but sometimes without immediately fatal results; in such cases damage is most probably caused by collision with wire fencing. Fracture of sternum.

(No. 1672.) A hen Grouse was "picked up alive" on a Berwickshire moor in August. She weighed only $14\frac{1}{2}$ ounces, and was very thin and in very poor feather; but upon dissection it was found that, perhaps a month or two before, she had broken her breastbone right across by collision with something—probably a wire fence. The smaller posterior portion had been displaced

forwards and upwards, riding upon the larger portion, and there becoming fixed firmly by osseous union, but with a considerable amount of displacement

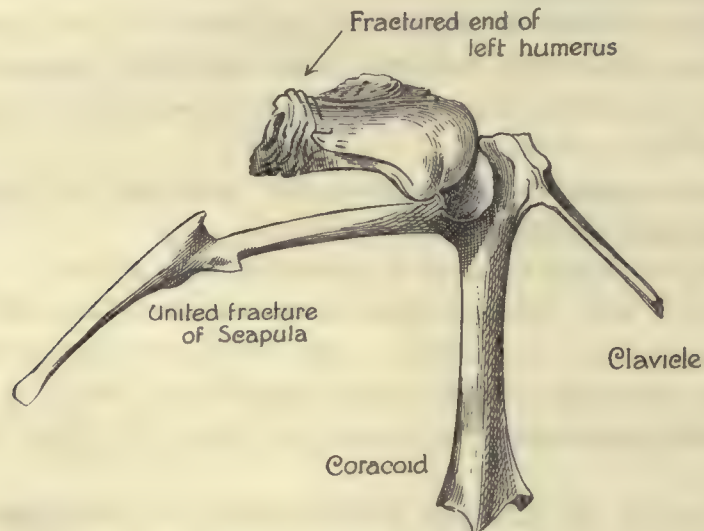


Fig. 1., No. 301. A permanently fractured left humerus and a fractured and reunited left shoulder blade.

and shortening (see Fig. 6). This accident must have completely disabled the bird for six weeks or a month, rendering her quite unable to fly. Yet

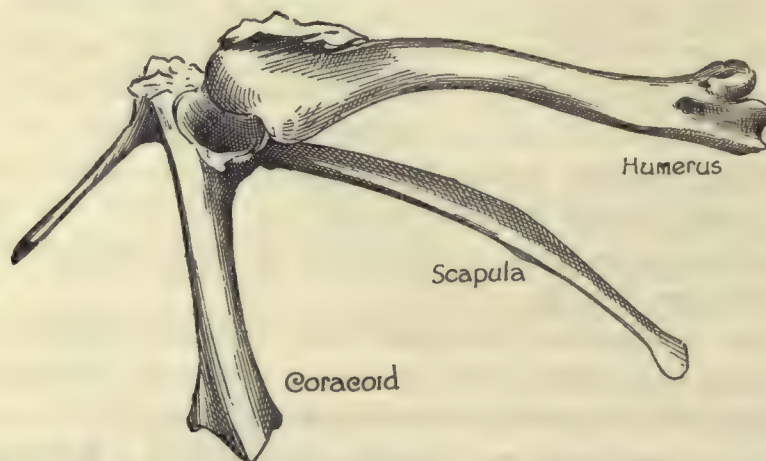


Fig. 2, No. 301. The same bones uninjured from the right side of the same bird.

she had lived, and the broken bone had united. The only apparent disability remaining was the infestation with parasites, *Hymenolepis*, *Davainea* and *Trichostrongylus* having all established themselves in excessive numbers in

the various portions of the gut. Thus Strongylosis would have eventually killed the bird, but only indirectly and as an after result of the injury, which in itself was cured.

(No. 1626.) A young Grouse chick, $11\frac{1}{2}$ ounces, very plump and well feathered, was found dead in Argyllshire, August-1908, and was forwarded for examination.

There was no sign of disease, the bird was in excellent condition, and death had resulted from collision, probably with wire fencing, which had broken the breastbone right across. There was hardly any external sign of damage in this case; but on removing the skin the bruising and bleeding which overlay the more serious damage beneath at once indicated the cause of death.

It is easy to distinguish between damage before and after death, when it is remembered that the circulation is active in the former case and inactive in the latter. Any violence done before death is accompanied by bruising and bleeding. Damage done after death may be accompanied by *post-mortem* staining due to the leakage of bloody serum; but will never show blood-clots lying under the skin or amongst the muscle-sheets or other organs.

(No. 1824.) A hen Grouse, of 20 ounces, was "found dead, but quite warm, about a mile from the nearest part of the moor, and at a place ^{Fracture of vertebrae.} down to which Grouse never go unless when driven off the moor by storm, which very rarely occurs." This was in Cumberland in March 1909. The bird was quite healthy, in good condition, well feathered, and of a fair weight, and having been found dead with feet and legs well feathered, was just the kind of bird to be classed as a case of "the acute form of 'Grouse Disease' which kills off birds in splendid condition before they have time to waste." But there was some blood in the mouth, and when this clue was followed up by further dissection the root of both lungs was found to have been torn to pieces by splinters of bone from the fracture of two or three vertebrae. There was a fair number of *Trichostrongylus* in the caeca, but no sign of disease and no tapeworms.

(No. 1762.) A cock Grouse of 26 ounces was forwarded from Scotland with the correspondence quoted below. The case affords an excellent ^{Internal injuries.} example of the evidence upon which the idea of an acute and very rapidly fatal form of "Grouse Disease" has been founded.

The gamekeeper writes as follows :—

“I am herewith sending you a Grouse cock which, I think, must have ‘gapes’ or something. His neck is very much swollen. This is the third bird of the kind I have seen during the season. We are now seeing diseased Grouse, at least birds having all the appearance of such. In fact, taking all over I never saw worse feathered birds than those we get here. They are especially poorly feathered on the legs.”

This was written at the end of September when the birds were in full moult. This particular bird had still the old claws on, and two primaries of each wing to shed; and the feet, though apparently unfeathered, were on closer inspection just beginning an excellent growth of young feathers. One of its eyes was damaged. Attached to the bird was a note saying that it was a diseased Grouse, notwithstanding that it was making a healthy moult for the winter, and weighed 26 ounces. On dissection the swelling of the neck was found to be due to a mass of loose blood-clot; the thorax also was full of blood-clot, and the bruising and tearing of the blood-vessels about the root of the neck left no doubt that the bird had met with an accident. There were no tapeworms in the bird at all, and no sign of disease of any sort. And though the cæca contained a good many *Trichostrongylus*, there was no redness, and the mucosa was quite healthy.

(No 1841.) A cock Grouse, 18 ounces, found dead on arable land. April 1909, Perthshire. Two or three others had been found there lately, but in this one, which was sent for examination, there was such profuse bruising and so much effusion of blood about the neck and throat that there was no doubt that the cause of death was accidental. *Trichostrongylus*, however, was very abundant in the cæca, though there was no redness of the villi; *Davainea* was present in large numbers.

(No. 1838.) A cock Grouse of 20 ounces was forwarded from Haddingtonshire in April 1909, with two others, definitely showing signs of advanced Strongylosis. This bird, however, had the lungs torn before death by pieces of broken rib, and there was blood in the mouth and trachea. In the absence of any note to the contrary this damage could be accounted for by the bird having been injured by a dog when picked up alive. But, as the bird was found dead in this condition, the damage probably occurred by collision with a fence or some accident of a similar kind.

(No. 1397.) A hen Grouse of 26 ounces found dead and in excellent condition,

on May 5th, 1908, was brought for examination as a case of the acute form of "Grouse Disease," by a keeper whose birds were actually at the time dying in large numbers from Strongylosis. But this bird was found upon dissection to have a rent in the abdomen, and a wound from some wire or fence, which had led to extensive internal bleeding. It was undoubtedly a case of accident, though the bird was fully infested with *Trichostrongylus*, and there was a considerable amount of villous reddening in the cæca. Had the hæmorrhage escaped notice, or had the bird been killed by some less obvious accident, it would have taken its place in the list of evidence which supports the belief in the acute and very virulent form of "Grouse Disease" which kills birds before they have time to waste.

(No. 1296.) A cock Grouse of 21 ounces was "watched for ten days" in March 1908. During that time he was flushed regularly every day by the gamekeeper at the same place. But during the last few days he could not be flushed "without the help of a dog as he was becoming every day the weaker"; so he was shot, and forwarded as a case of "Grouse Disease." This he was, but only to a very slight extent. The real reason why he objected to being flushed regularly every day was because he had retired to a certain retreat to be away from other birds and remain quiet while a wire-fence wound healed. It was found that the wire had torn through the skin of his breast, and had rent the pectoral muscles, which are the muscles of flight. Had he been left alone he would have recovered in a few weeks, and would have rejoined the healthy birds on the higher ground as soon as he was fit to hold his own. This retirement of a sick or damaged Grouse to a place where he can recruit his health in solitude is in accordance with the habit of almost every animal that lives.

Flesh
wound
from
barbed
wire.

(No. 1604.) A cock Grouse of $17\frac{3}{4}$ ounces was found dying in Yorkshire in July 1908 with a bad rent in the flesh of the breast, bleeding freely. It was to some extent also suffering from Strongylosis.

Two cases of fractured sternum have occurred in Blackgame, forwarded for examination.

No. 1234 represents a recent fracture of the sternum in a Blackcock. No. 1232 (*see* Fig. 3) represents almost exactly the same damage reunited, owing to the fact that the Greyhen, in which it occurred, did not die until some months after the accident. The exact method of overriding and union of the broken bone in this example is shown in Figs. 4 and 5

which give a view of the breastbone from each side. Both cases occurred in a very curious series of six deaths in Blackgame which were forwarded for examination as cases of "Grouse Disease," all coming from the same locality.

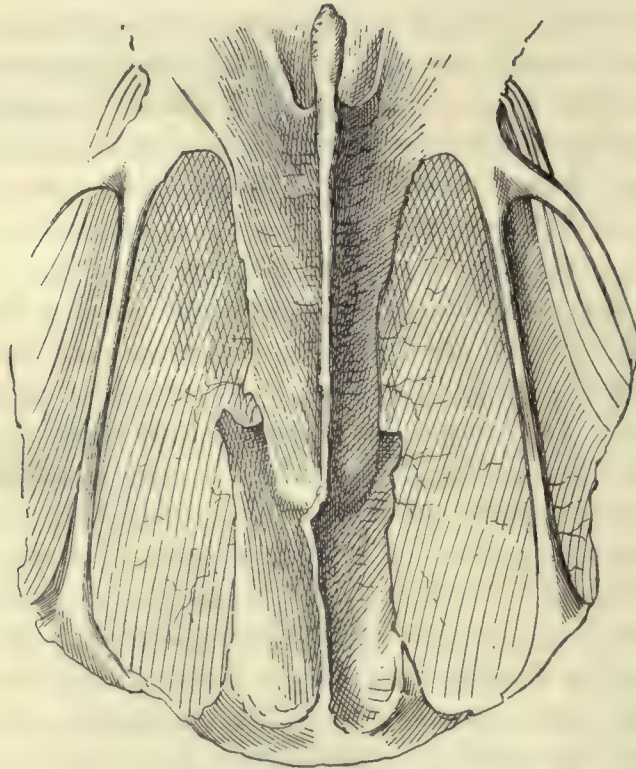


Fig. 3, No. 1232. The breastbone of a Greyhen fractured and reunited.

The facts were as follows:—

(No. 1.) A Blackcock, October 16th, 1907; weighing 45 ounces; was found dying; in excellent condition. Had been feeding on corn.

Remarkable
series of
cases.

(No. 2.) A Greyhen, October 26th, 1907; found dying, thin, in poor condition, dirty beneath, and much bedraggled; had evidently been squatting for a long time on the ground, unable to fly. This bird was forwarded by train for examination, and on arrival was still living. She was kept alive, feeding freely on grapes, until November 2nd, when she was killed with chloroform, as there appeared to be some internal damage with a complete absence of any sign of disease. On *post-mortem* examination the breastbone (Fig. 3) was found to have been broken right across near the abdominal end; but it had since become firmly

united again with a little displacement due to overriding of the hinder fragment (*see* Fig. 6). Clearly this bird was unable to fly because the wings from long disuse had become weak, and adhesions about the pectoral muscles probably made the attempt to use them painful. The joints of the legs too were stiff and difficult to straighten, the result of long squatting on the ground amongst wet undergrowth. She must have led a sedentary existence for some time, and would probably have died without regaining the power of flight. There can be no

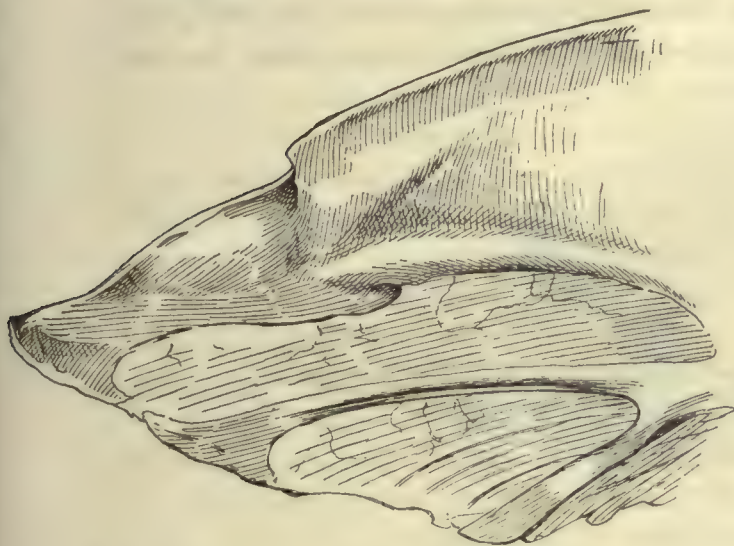


Fig. 4, No. 1232. View of the right side of Fig. 3.

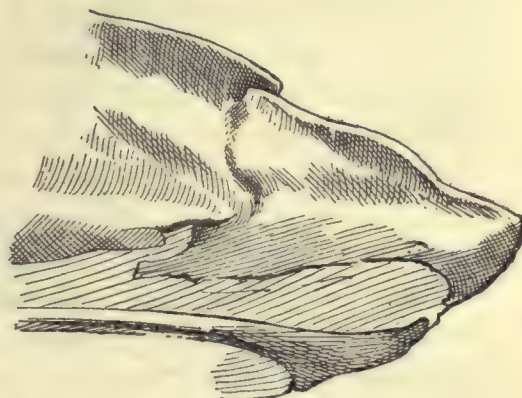


Fig. 5, No. 1232. View of the left side of Fig. 3.

doubt that the cause was collision, probably with a wire fence. The organs showed no sign of disease.

(No. 3.) A Greyhen, weighing 34 ounces, was found dead in good condition ; had been feeding on corn. Examination showed that an old wound had produced extensive bleeding in the abdomen, but so long previously that the clot was semi-organised and formed a series of concentric blood-cysts. A more recent damage had caused extensive bleeding around the base of heart and into the lungs, and this had killed the bird ; but not until several hours had elapsed since the accident, which almost certainly resulted from collision with a fence. There was no sign of disease.

(No. 4.) A Blackcock, weighing 41 ounces, was found dead on November 1st, partly picked by crows or mice, but in fair condition. It had been feeding on

hawthorn berries. This bird had a deep wound in the breast, from an accident which had broken the lower end of the sternum. The damage was undoubtedly the result of collision with a fence, or something of the kind. It was exactly comparable to that in the Greyhen, No. 2, but more severe, so that the bird died shortly after the accident. No sign of disease was discovered.

(No. 5.) A Blackcock, weighing 39 ounces, was found dead in good condition on November 4th. No food in any part of the gut. This bird had its back broken, and the bone splinters had torn the lungs and the smaller air-passages, so that they gradually filled with blood. The hinder part of the bird's body and its legs must have been paralysed, so that it could not search for food,

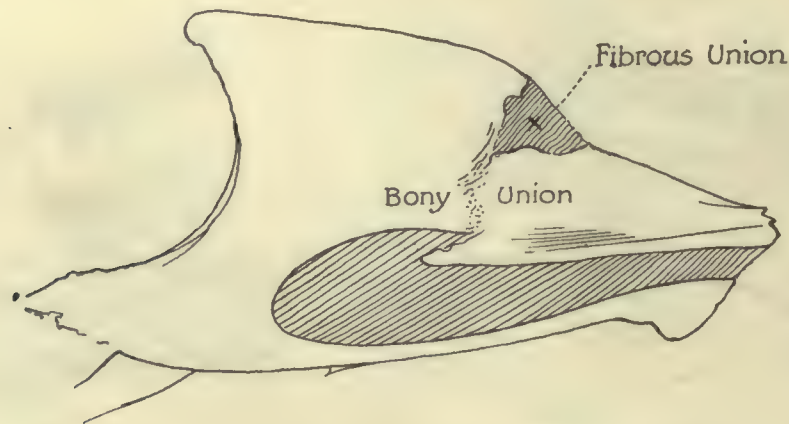


Fig. 6. Showing method of union of broken breastbone.

and the drowning of the bird in its own blood took so long to kill it that all the food eaten before the accident was digested, and the remains passed. The whole body was full of venous blood, showing that twelve or twenty-four hours may have elapsed between the accident and the bird's death, which was due again almost certainly to collision with a fence. Once more there was no sign of disease.

(No. 6.) A Greyhen, weighing 31 ounces, was found dead on November 4th in good condition; again the back was broken, but this time lower down at the level of the last rib instead of at the fifth rib as in No. 5. The left lung was compressed and rendered absolutely useless by a large blood-clot which had collected in the thorax owing to internal damage caused by the splintered bone. This bird had evidently lived for some hours after the accident, and had

previously been feeding on corn. There was no sign of disease, and every reason to suspect collision with a fence as the cause of the accident.

Obviously this series of deaths was not due to an epidemic of disease, though it is difficult to understand why so many birds should have collided with fences in the same locality, where no new wires or other obstructions had been recently erected. The gamekeeper's view at first was that they all had disease, and outward appearances to some extent supported him. Later on, however, the Blackgame began to leave the valley where they had been feeding on corn, and where the accidents occurred, and once more took to the moors. The keeper reported that the Blackgame on the moors were quite healthy, and continued: "I have been among Blackgame and Grouse for over forty years, and I never saw Blackgame affected the same way. If eating green oats is killing them, they have eaten them for over forty years and were not a whit the worse. I have known Blackgame eat oats from September to December, and not a single bird die from it. What puzzles me is why they are not dying in the next valley (3 miles off). When the Blackgame light on the ground they tumble on their heads. If there is a fence hard by they sometimes fly into it. I have seen many birds (recently) showing the same symptoms."

All this suggests some form of intoxication, and it is just possible that the sodden and half-rotten grain eaten by the birds might produce sufficient alcohol by fermenting in the warmer process of digestion, to act upon them in this way. There is, of course, also the possibility that grain soaked in spirit had been purposely put down, but in this case it was improbable.

It was certain, at any rate, that the epidemic was an epidemic of accidents and not of disease, however suggestive appearances may have been to the contrary.

(No. 1627.) A cock Grouse of 21 ounces was caught and killed, July 1908, in Argyllshire. There was very great dilatation of the crop, which was filled with an old blood-clot and with heather, the crop contents had been there for a long while, and had become dry and mildewed. There were two or three cicatrised wounds through the skin and crop; but these were all closed except one, which remained open and suppurating. The passage to the œsophagus downwards was free, and the bird might possibly have recovered in time. The crop was adherent everywhere to the subcutaneous tissues, and so to the skin. And there were numerous enlarged blood-vessels wandering both over the crop wall and also in the adhesions as the result of

Damage to
crop by
barbed
wire.

the diffuse inflammation. It is extraordinary that the bird should so well have maintained its weight—21 ounces; *Davainea* was absent, *Hymenolepis* and *Trichostrongylus* were both present, but with no redness in any part of the gut.

No. 684 is an example of recovery from a fracture of one of the wing-bones in a cock Grouse. The radius in this case had been broken in two at the junction of the middle and lower thirds, probably from a shot wound. The bird must have lived for at least a month or six weeks during the winter without flying, but made a perfectly sound union notwithstanding, and survived to be shot dead on the wing in April as a healthy bird killed for purposes of crop analysis (see Fig. 7).

Fracture of
radius from
shot
wound.



FIG. 7, No. 684.



FIG. 8, No. 287.



Broken and re-united wing-bones.

No. 539 is again an instance of the radius being broken in two pieces at about its centre, probably by shot. In this case there was also some evidence of periostitis in the ulna at the same level. The union was incomplete when the bird was killed; but, though some movement was possible between the broken ends, the formation of callus and new bone had made a considerable advance towards effecting a firm union.

No. 287 presented a firmly united fracture of the radius which had been broken in two about the centre. There was no evidence of damage to the ulna. A shortening of 2 mm. (from 50 mm. in the sound bone to 48 mm. in the

damaged one), occurred in the united radius, and union was effected irregularly with a large boss of new bone (see Fig. 8). This bird was an undersized hen, killed as a "piner" on August 15th, 1906, and suspected of disease. She was shot on the wing, but was in very poor condition and badly infested by *Davainea*, *Hymenolepis*, and *Trichostrongylus* within, and by innumerable bird-lice and other parasites without.

Nos. 434, 984, 1250 (see Figs. 9, 10, 11), all resemble one another in



FIG. 9, No. 434.

FIG. 10, No. 894.

FIG. 11, No. 1250.

Broken and re-united leg-bones.

representing united fractures of the upper third of the tibia and fibula. In each case the fracture was comminuted. The shortening in one leg is from 83 mm. to 76 mm. The union in each was effected by an irregular and immovable mass of bony matter thrown out to include the fibula which is also greatly thickened.

Damage to
leg-bones
by shot
wounds.

No. 434 was a cock bird which lived to be shot on January 7th, 1907, weighing 20 ounces. The fractured end of the bone had been rendered smooth by absorption, and the deformity caused by overriding of the lower fragment.

had been partly obliterated. In No. 894 the upper fragment was united to the lower at an angle of 30 degrees. No. 1250 was also a cock, found dead in November 1907, having succumbed to *Strongylosis*. The shot which caused the damage can be seen to the left impacted in the bony mass.

No. 1304 was a cock Grouse of 18 ounces, caught alive in poor condition, but in fairly good feather. It had evidently met with an accident. There appeared to have been a shot wound in the back, but the chief damage was in the leg, which was dislocated at the tibio-metatarsal joint, and one central toe

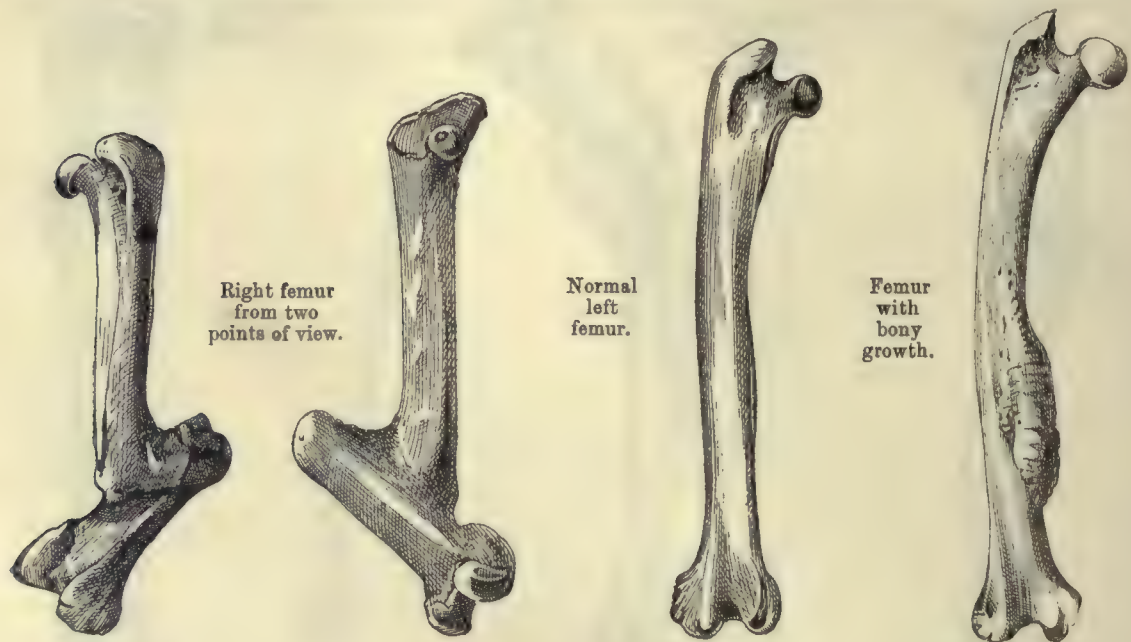


FIG. 12, No. 696.

FIG. 13, No. 696.

FIG. 14, No. 696.

FIG. 15, No. 998.

Broken and re-united thigh bones.

was also damaged. These injuries may have been secondary to the shot wound, and may have resulted from a heavy fall; but the bird had survived, and would have recovered with some deformity. It was, however, a rather advanced case of *Strongylosis*, and badly infested with tapeworms also, both *Davainea* and *Hymenolepis*.

Two cases of damage to the femur may be mentioned:—
Fracture of femur.

No. 696, a united fracture with shortening from 55 mm. to 43 mm. owing to the excessive displacement of the lower portion of bone. The upper fragment forms an angle of 45 degrees with the lower (see Figs. 12, 13).

The bird was a hen found dying from Strongylosis in April, but the fracture must have taken place at least six weeks before. From the complete union effected the bird must have been healthy at the time, but the accident may have been the starting-point of sickness, which resulted eventually in its death. Fig. 14 shows the undamaged femur of the same bird.

No. 998 shows a bony outgrowth of the femur due to periostitis resulting probably from some violence which was insufficient to break the bone (*see* Fig. 15).

No. 1757 was an adult cock Grouse of 16 ounces only, found in Nairnshire in September 1909, sick and unable to fly. It was a bad case of Strongylosis; but the original cause of its sickness was a number of lead pellets which had some time previously passed through the pectoral muscles, the sternum, and the liver. Internal
shot
wounds.

No. 1739 was an adult cock Grouse of 18 ounces, in good feather, but found in Yorkshire on September 5th, 1908, sick and unable to fly. The bird was suffering from Strongylosis; but there were also healed scars of shot-pellet marks. The lungs were somewhat stained *post-mortem*, but one of them was thick and solid. It was in part a dark, rich, reddish black all through, and in part normal pink. A line of adhesions joined up the second and third lung-lobes, and there were cicatricial puckerings showing where a shot had passed through. The solidification was due to old bleeding. A shot had also recently passed through the neck, traversing the muscles, and tearing a small hole in the trachea, which had remained unhealed. There was bloody fluid in the mouth and trachea. The skin wound, however, had nearly mended, but bits of feather were found in the tissues of the neck, and the scar outside was matted up with broken feathers. The skin wound made by the shot which passed between the ribs and entered the lung had completely healed, and its position only was shown under the skin by a small blood clot which persisted. This bird must have survived its most recent wounds for a week or two at the least.

No. 1923 was a cock Grouse of 20 ounces, which was sent for examination from Perthshire in very good condition.

The following information was sent with the bird :—

“I enclose a Grouse which I picked up to-day. I put up a pack of Grouse. This one rose a little after the others, and after flying about 200 yards dashed to the ground, and when I got up to it it was quite dead and blood flowing from its mouth.”

Examination outside before opening revealed the fact that the bird had been

pricked by shot. One of the quill feathers was cut through, evidently by a pellet, and there were marks of shot in other quills. Blood was flowing from the mouth, and an examination of the lungs showed that one of them had been torn by shot so that many of the air-passages were full of blood. But the blood liberated by the original wound had clotted in the lung and saved the bird from immediate death. Had the bird been allowed to rest until this lung and its clot had healed and become firmly cicatrised it would perhaps have recovered. Instead, however, it was flushed and forced to take flight. This broke down the freshly formed clot, and the bird died of secondary hæmorrhage. There was in addition to this a very large clot round the liver, showing that a pellet had entered this organ also. This case is a very good example of what has certainly been described in former years as the sudden death of birds from acute disease, which strikes them down in the pride of health in full flight and excellent condition. It is also a very remarkable case of long survival after serious damage caused by shot wounds.

No. 1260 was an adult cock Grouse of 19 ounces, found dead on January 3rd, 1908, in Argyllshire.

This bird had been badly sprinkled with shot some time before its death—at least a couple of months, judging by appearances. That it should have survived at all is extraordinary.

Three shot pellets were found lodged in the tissues of the neck; two ribs had been broken on each side, and had firmly united again. There were small caseous masses in the lung, the remains of small localised abscesses which had been caused by the passage of the shot. The pleura were fastened to the ribs by traumatic adhesions; and as the result apparently of some obstruction or damage to the usual set of veins there was a great enlargement of what are generally quite insignificant veins in the wall of the proventriculus. This swelling, however, is purely vascular, and a different thing altogether to the swelling in the two cases just described. It has in this respect some similarity to the case which follows, a case in which the increased vascularity of the proventriculus also resulted from damage to the thoracic viscera.

No. 1279 was a cock Grouse of 23 ounces, found dead on February 17th, 1908, in Inverness-shire. It was in excellent plumage and condition, and although an abundance of Strongyles was to be found in the cæca there was no redness and no engorgement of the villi.

The cause of death was apparently collision in flight, and the chief damage

was that suffered by the heart, which was much enlarged and swollen out to twice its normal size by a great extravasation of blood in the muscular tissue of the walls, both of the auricles and ventricles. The veins running in the wall of the proventriculus were much engorged. The lungs were unhurt, and otherwise the bird was perfectly normal.

No. 1899 was a hen Grouse of about 17 ounces, found on July 23rd, 1909, in Sutherlandshire, sick and unable to fly. It was in very poor condition, and heavily worm-infested. But the chief cause of distress was a very large tumour caused by an aneurismal-like rupture of the vessels in the inner walls of the gizzard. The cavity of the gizzard was enormous, and the organ occupied nearly the whole of the abdominal cavity, causing complete compression of most of the intestines intensified by the formation of adhesions due to peritonitis and the stretching of the normal mesenteries over the tumour. The tendinous and tougher portion of the gizzard had retained its normal size and shape, but the fleshy part had become greatly distended. The tough lining membrane was the part which had given way.

Tumours
caused
by shot
wound.

No. 1177 is probably a case of a dermoid cyst situated in the neck, though the cyst simulates the occasional result of a shot wound in which small fragments of feather are enclosed in a caseous mass in the connective tissue between the skin and the crop. The crop in this case was not damaged. Scraps of feather formed the nucleus of two tumours 35 mm. and 15 mm. in diameter respectively. The sebaceous matter, of a golden yellow colour, was in concentric layers, enclosed in a thick fibrous envelope with innumerable blood-vessels covering the outer surface, and supplying the cyst wall with blood.

No. 1159, a hard fibroid tumour $1\frac{1}{2}$ inches (45 mm.) in diameter, protruding from the foreneck of this bird. The nucleus again was a fragment of feather, and this occupied a small abscess cavity in the tumour with a sinus leading to the outside of the skin. The tumour was covered by bare, rough, and rather thickened skin, devoid of feathers, and resulted probably from a shot wound. There was no connection with the crop.

Various accidents may happen to the foot and metatarsus of the Grouse, ranging from complete loss of the foot at the tibio-metatarsal joint as in No 437, to the loss of toes at the metatarso-phalangeal joints, or at the various inter-phalangeal joints as in No. 970.

Damage to
feet.

Steel vermin traps will perhaps account for some of these cases, but in No. 970 the appearance of the stumps of toes on both feet, to a different

extent on each foot, suggests frost-bite as the cause; or at any rate some form of gangrene rather than steel traps. A likely explanation is the strangulation of toes, sometimes even of feet, in infancy by the tightening of strands of sheep's wool accidentally wound round them. This is a common accident with Lapwings.

An instance of the death of Grouse in a vermin trap may be recorded, in which two healthy cocks fighting in the spring accidentally came together into a "Samson" trap, and were simultaneously killed.

No. 1606, a cock Grouse of $18\frac{1}{4}$ ounces, was found dead on July 13th, 1908. There was a very little *Calluna* heather and Blaeberry leaf and stem in the crop. The bird had probably found difficulty in obtaining sufficient food for the lower bill was split and curved, forming an unhandy instrument for plucking heather. The death by starvation, however, had been hastened by Helminthiasis. *Davainea* was abundant; *Hymenolepis* filled the duodenum, which was purplish red, very congested, with engorged villi within, and engorged venules without; while the cæca were excessively congested within and without, and *Trichostrongylus* was present in great numbers. This bird would very probably have recovered during the summer but for the additional handicap of its damaged bill. It had survived the two months of highest mortality, April and May.

Many interesting cases have also been recorded of recovery from flesh wounds either by shot, or by barbed wire, and the following have come under the notice of the Inquiry:—

No. 1242 represented a long standing leakage of the crop, due to a wound through the skin and crop-wall. Owing to constant use of the crop, and to the alternate distension and contraction of the overlying skin, the adhesions between the edges of the skin and crop-wall had become permanent before there was any chance of the openings in either being closed. Bits of heather pressed constantly between the lips of the wound had prevented healing, and had defeated the efforts made by the crop to pass all the food into the gizzard. The bird had therefore to eat more than the normal amount to make good a chronic wastage, and this accounts for the very abnormal distention of the crop which often characterises cases of the kind.

No. 1627 is another case of the same nature.

Either or both of these last two cases may have resulted from shot wounds,

or from rents made by barbed wire. The latter is probably the cause in the majority of cases.

It is fairly common to find shot pellets loose among the contents of the crop or in the gizzard. They have sometimes been lodged there when the bird was killed, but have more commonly been picked up and swallowed as grit, or out of simple curiosity. In one case a shot pellet was actually encysted in the thin wall of the crop. It would have found its way eventually into the crop without any damage; but it is at least curious that a pellet having entered the bird with sufficient impetus to get through the skin and half way through the wall of the crop should not have gone right through into the contents.

Shot frequently found in crop.

No. 1150 is a similar case resulting from a shot wound; the pellet had entered the body of the bird, and having perforated two portions of the gut had then lodged in the gizzard. Localised peritonitis had followed, causing abundant adhesions, and a short cut had been established between the gizzard and the main intestine as well as another from the upper portion of the main intestine to a lower portion of the same.

The danger to young chicks in sheep drains and in moss cuttings for "peats," or for general surface draining, has already been mentioned. It is greatest during a "spate" after a spell of dry, hot weather in June or July, when young broods have been led by their parents to take shelter from the sun in dry drains cut with steep sides. The sudden filling of these drains is responsible for the loss of many chicks before they find a place to scramble up into safety. This danger is well recognised, and the best method of avoiding it is dealt with in another chapter.¹

Danger of sheep drains.

Accidental poisoning is a rare cause of death in Grouse. A few cases have been brought before the Committee as cases of "Grouse Disease." It is not easy to guess how poisoning occurs, for poison used in killing vermin is administered mainly in eggs, and in the carcasses of fur-bearing animals, neither of which are likely to be tampered with by Grouse. Poisonous sheep dip has been blamed in some cases; but it is difficult to believe that it can be more than the rarest cause of accident.

Accidental poisoning.

The theory that many Grouse are poisoned by lead pellets, whether swallowed as such, or in solution as carbonate of lead in drinking water has been ingeniously upheld by an elaborate calculation of the amount of shot scattered over a moor

¹ *Vide* chap. ii. p. 15.

in a shooting season; but though the crops and gizzards of Grouse do occasionally contain a lead pellet or two, they are sufficiently uncommon to be a matter of curiosity to the finder rather than a cause of sickness to the birds.¹

The following is an account of what was supposed to be accidental poisoning of Grouse by sulphate of Barium. It is given by Macpherson in the "Fauna of Lakeland."² Quoting John Borrow as writing from Alston in 1837, he says: "In consequence of the Grouse in some parts of this neighbourhood having been unable to procure sand (owing to the depth of snow), they have picked up particles of the sulphate of Barites, which appears to have been the cause of a very great mortality among them. A person whom I can depend on assures me he saw not less than forty brace dead upon the moors a few days since."

One may, I think, legitimately wonder whether this mortality was not due rather to a grit-starvation, accompanying and augmenting the evils of food-starvation, which is always present to some extent with deep snow.

The Rev. E. A. Woodruffe Peacock gives cathartic flax as a cause of death by violent purging to young Pheasants; but no case of poisoning in Grouse can be attributed to the consumption of any plants found growing upon a moor.

Several cases of abscesses and septic poison of the leg, which resembled "bumblefoot" and "whitlow," were sent up for examination during 1908 (*see* Plate XXXII.).

No. 1681 was a cock Grouse of the year, shot purposely on August 25th, 1908, on account of the condition of its body and feet. The foot of another Grouse was affected in the same way though to a less degree. This bird weighed 15½ ounces, and its condition was fair. Both feet were much swollen with collections of caseous pus. The figures shown on Plate XXXII. were drawn from the bird when quite recently dead. It was killed "on an exceptionally dry juniper hill" in Inverness-shire. There were no abnormalities in any other part of the bird, except the usual infestment of *Trichostrongylus*; but the organs were all apparently healthy.

No. 1744 was an adult cock Grouse shot in September, in Perthshire, weighing 19½ ounces, and somewhat thin. It exhibited the usual infestment with *Hymenolepis*, *Davainea*, and *Trichostrongylus*, but was otherwise healthy except for a swelling of one of the toe joints, very similar to the case just described (No. 1681), but not symmetrical.

¹ *Vide* Macdonald, "Grouse Disease," p. 160.

² *Vide* Reverend H. A. Macpherson, "A Vertebrate Fauna of Lakeland," p. 323. Edinburgh: D. Douglas, 1892.

Left of
Chlorophanes



Left Foot



Left Foot

"BUMBLEFOOT" IN GROUSE



Right Foot

B. Wilson, Cambridge

No. 1675 was a young bird of the year, shot in September, on the same moor in Inverness-shire which produced No. 1681, and another similar specimen which was not forwarded. All came from a very dry, healthy, juniper-covered valley, and all had appearances much resembling the disease known to poultry farmers as "bumblefoot."

No. 1918 was an old hen Grouse killed in Yorkshire, which weighed only $13\frac{3}{4}$ ounces, and was exceedingly thin. This bird had a swollen knee of the same character as the above, and there was some evidence that it was an old standing trouble, for the claws on the foot of the damaged limb were of an abnormal length, whereas those on the foot of the sound leg were broken and worn to stumps by the extra amount of wear and tear. The feathers of the left undamaged leg were similarly much worn, whereas those on the damaged leg were in good condition. The bird was suffering from Strongylosis, the cæca being very much congested and full of *Trichostrongylus*, and the villi very red. There was an old blood-clot over the liver, which may have resulted from a stray lead pellet, and the swelling of the knee joint in all probability should be attributed to damage by another pellet which may have struck the bird at the same time. In poultry farming "bumblefoot" is the name given to any form of abscess in the foot, and as the abnormal structure of the ^{Bumble-foot.} Dorking's foot with its extra toe made this breed particularly liable to have a suppurating corn or other accident of this nature, it was considered at one time to be almost peculiar to that breed.

It is evident, however, that in the Grouse which have been considered above, and in the poultry affected with "bumblefoot," we have generally the result of localised suppuration from septic infection, following upon some small and unnoticed wound or damage such as a scratch or bruise. A "whitlow" is exactly comparable to this affection in the toes, and a whitlow may be a septic affection of the superficial or deeper tissues, and if of the latter, the infection may spread to tendon sheaths, or even into the joints themselves, or upwards between the muscles.

In the Grouse above mentioned the suppuration is more or less localised, and the pus, having no free exit, has become caseous in the lapse of time, hence the firmness of the swellings.

B.—*Causes of Death and Damage resulting from Natural Conditions.*

Nearly all the causes of death and damage due to purely natural conditions have from time to time been so well described that it will here suffice merely to recapitulate them.¹

1. Climatic extremes are well known and well recognised. They may occur from the time the eggs are laid to the end of the bird's life. At every age, in every season, and every year, the welfare of the bird is threatened by excess in one direction or another.

Excessive heat and its usual accompaniment, water famine, are both somewhat uncommon at the time of year when they would be most dangerous to Grouse life. They are referred to in chapter ii.²

The following abstracts sum up the harm done by wet and cold. Macdonald in "Grouse Disease" has no doubt about the matter when he writes that "Damp and cold never fail to produce diarrhoea, cramp, and disease"; and again, "Excessively cold or wet seasons are succeeded by great mortality among birds, and Grouse suffer more in wet than in dry seasons, however cold—this was strikingly demonstrated in the wet season of 1872-1873"; and again, "Cold wet causes bad hatching seasons."³ So also Macpherson in the Fur and Feather Series says that young Grouse "do best in fairly dry seasons."⁴ And for the bad effect of cold and wet on the food supply Macdonald, again, in "Grouse Disease," says: "We can also connect the disease with wet seasons. The heather does not quite ripen, particularly the small tops on which Grouse chiefly feed."⁵

There seems, in fact, to be a consensus of opinion amongst those who have had the best opportunities for judging, that the hatching season can hardly be too dry so long as there are dewy nights. The chicks can supply their needs by drinking dew in the morning, and beyond this they find sufficient moisture in the insects and young succulent moss-capsules and heather shoots which form their staple diet, and which contain something like 60 to 80 per cent. of water. The sitting hens want water and must have it, and their bulky droppings may

¹ In connection with the effect of weather conditions upon Grouse, much additional evidence has been collected by the Committee, and is summarised in Appendix G., vol. ii. In view of the information now made available for the first time, it may become necessary to reconsider some of the opinions of recognised authorities referred to in this chapter.

² *Vide* chap. ii. p. 16.

³ Macdonald, "Grouse Disease," pp. 24, 40.

⁴ Fur and Feather Series, "The Grouse," p. 24.

⁵ Macdonald, "Grouse Disease," p. 40.

always be found on the edges of the burns and springs nearest to their nests. They are reported to suffer seriously in a drought. But when all is said, excessive heat and drought are far less to be feared in the British Isles than excessive wet and cold. Sunstroke, "staggers," and "splanders" in wild birds of any kind are extremely rare when compared with the results of an excessively wet hatching season, especially if it happens to be accompanied by cold. Too much wet is undoubtedly more harmful both to the sitting hens, to the eggs, and to the young birds when hatched, and for a month at least after hatching, than any other climatic extreme to which Grouse are subject.

Excessive rainfall is said to account for the scarcity of Grouse on the moors of the west of Scotland and of the Western Isles, and to this John Colquhoun adds that "Grouse are never so plentiful on the west coast, from the wet springs addling so many of the eggs." And again, "Protect as strictly as possible, and kill every rapacious bird and beast on the ground, there never could be half as many Grouse reared in the west as in the north or centre Highlands; and the reason is the humid climate prevents it."¹

"Every sportsman knows that the Grouse in the north or centre Highlands of Scotland are immensely more numerous than in the watery west."²

The nesting season of 1906 was most typically a bad wet season everywhere, and in walking over some of the Scottish moors, south of Perth at any rate, nest after nest was found to be deserted with a full clutch of eggs in which the chicks had died just before the time of hatching. Second broods are in such cases no doubt produced, but if an early winter sets in, or if the autumn turns wet and cold, these late-hatched broods swell the ranks of the poorly-feathered, undersized birds which appear in spring as "piners," and are liable to succumb eventually to disease of one sort or another.

The question of the diminished value of second broods is fully discussed in another part of this Report.³

In every way, except in checking the growth of the heather, hard frosts and heavy snow do less harm than excessive rains. A certain number of hens may be occasionally frozen to death upon their nests, as has been recorded by Stuart-Wortley (Fur and Feather Series). Eggs, too, may be "frosted" when late frosts are sufficiently severe,⁴ or young Grouse

Excessive
wet a great
danger.

Second
broods and
late birds.

Effect of
frost, etc.,
on food
supply.

¹ Colquhoun, "Moor and Loch," vol. i. pp. 194-198.

² *Ibid.*, p. 198.

³ Chap. xxi. pp. 469 *et seq.*

⁴ W. A. Adams, "Twenty-six years' Reminiscences of Scotch Grouse Moors," p. 94. London: Horace Cox, 1889.

may be killed by late snowstorms, as in 1864 on Glenshea; but such occurrences are very rare. The power of resistance of the egg to frost is dealt with in another chapter.¹

Still, however little direct harm excessive cold may do to Grouse, the indirect harm is often very great, and there is no doubt that late frosts in the north of England and in the south of Scotland, catching the heather after the sap has begun to rise, often reduce the available supply of food.

It may be well to review what has been written from time to time as to the effect that "frosted heather" is supposed to have upon the Grouse.
"Frosted
heather."

In Macdonald's "Grouse Disease" a Scottish forester is quoted as having stated that during a certain epidemic there was no "Grouse Disease" all along the sea coast where the heather does not suffer by frost, while 10 miles or so inland, beyond where the sea exercised its influence, there the "Grouse Disease" began. It is there stated that the dissection of Grouse that had died of the disease proved that their crops contained frost-bitten heather.² And, again, in a quotation from Colquhoun's paper, it is stated that in Perthshire, in 1852 and 1853, the heather was excellent, and in consequence there was no disease, while in 1854, 1855, and 1856 the heather was frosted without snow, and there was bad disease. Again in 1857 the heather was excellent, and there was no disease; and so on.³ Speedy, however, says: "Heather which has been killed by frost and entirely divested of its nutritive qualities is about the most unlikely thing for Grouse to feed upon."⁴ He says, too, that after bad disease there are more survivors on the high exposed heather-frosted parts of the moor than on the lower sheltered localities, and that "'Grouse Disease' has not been peculiar to those seasons when the heather was most generally frost-bitten, or when it had not been covered and protected by snow. . . . Some of the most fatal visitations have been preceded by winters more remarkable for mildness than severity."

The statements contained in the above quotations from Macdonald and Colquhoun are probably due to a misuse of the term "frosted heather," for there is a condition of heather which is *not* rightly called "frosted heather," and it will

¹ *Vide* chap. ii. pp. 10-12, vol. ii. Appendix H.

² Macdonald, "Grouse Disease," p. 40.

³ *Ibid.*, p. 122.

⁴ Tom Speedy, "Sport in the Highlands and Lowlands of Scotland," p. 202. Second Edition. Edinburgh and London: William Blackwood & Sons, 1886.

prevent misunderstanding if the meaning of the term is clearly defined. To begin with, young, fresh, green heather of the early summer may be caught by a late black frost which sweeps over the moor and literally "scorches" it red. This is a comparatively frequent occurrence in the north of England, and was well exemplified on a certain Yorkshire moor in the early summer of 1907. The countryside was green one week, and "as red as a fox" the next. Every leaf that was turned red by the freezing winds (there was no snow in the question) died, and eventually dropped off without recovering. But the plant was not killed; it very soon put out fresh leaves from the lower stalks, and the moor in a few weeks was as green as ever. Still, the fact remains that the birds of that moor were suddenly reduced from a very abundant to a very limited supply of food, for in no case will a Grouse eat such useless stuff, nor has a Grouse's crop ever been found to contain this fox-red frosted heather. It is dead, and the birds know it, and forthwith proceed to look for something that is not dead. They will not eat it, and therefore any harm that accompanies its appearance is due, not to the presence of this useless refuse, but to the sudden reduction of the wholesome food supply. Such fox-red frosted heather must on no account be mistaken for the dark, red-brown, winter heather, which is secure from any ordinarily severe frost, and is merely the resting condition of the healthy living plant. The two are totally distinct in colour, the former being, as has been said, brick-red or fox-red, and the latter a deep brown, or dark, reddish brown, often associated in the leaves of the other side of the twig, with a deep or vivid winter green. Such heather is alive and healthy, and forms perfectly wholesome food for the Grouse; it is, in fact, their staple winter food. ^{"Winter heather"} not frosted. The only point is that being somewhat dry and sapless (in which lies the whole reason of its immunity to frost), and lacking in food-value when compared with fresh, young, summer heather, about three or four times as much has to be eaten by the bird to get the same amount of nourishment. This dark, winter heather cannot be correctly called "frosted," since the change in it is merely due to a seasonal alteration in the chemical condition of the cell contents, while it remains in the healthy resting winter state. With certain modifications it may be stated generally with regard to the two forms of "frosted" heather that in the one case the heather is dead—having been killed by even a moderate frost—and that in the other it is living, and is proof against even a severe frost.

The presence or absence of snow on the ground makes a great difference in

time of frost. Snow acts as an efficient protection to the heather, and only the extra long twigs that protrude beyond the snow are affected by frost. Snow a protection from frost. Hard frost after snow trims the heather by cutting off and killing all the longer pieces, so that the leaves bleach whitish grey, and eventually drop off. This may happen even to straggling pieces of dark brown, winter heather if the frost is severe enough ; but it requires a very low temperature and a prolonged exposure to affect real winter heather to any great extent. There is no other condition of heather which can with any show of reason be called "frosted"; and it may be urged that no heather should be so named except that which has been nipped and killed beyond all chance of recovery. To call the resting condition of winter heather "frosted" is as unreasonable as to call any evergreen shrub "frosted" because its winter leaves are darker in colour than those which it produces in early summer.

Closely simulating the fox-red, frosted heather, however, is the heather damaged by a certain beetle known as *Lochmæa suturalis*. This pest Effect of heather beetle. has long been recognised in Argyllshire, Ayrshire, and Dumbartonshire, and its ravages were described by Mr Grimshaw in 1898.¹ This subject is also dealt with in the present Report.²

Before leaving the climatic causes of death and damage to Grouse, something remains to be said about heavy snow. Its most obvious danger lies, of course, Heavy snow. in starvation, since a heavy snowfall, unaccompanied by wind, and not followed by a thaw for many weeks, reduces the available food-supply to a minimum, and drives the Grouse to travel far and wide over cultivated lands, into gardens, town outskirts, and even to the seashore for a scanty living.

It is recognised that one of the best ways to help Grouse under such circumstances is to lay bare patches of heather by breaking through any hard crust that may have formed on the surface of the snow. This may be done either by rakes or harrows, and the spots chosen should be those where there is known to be the best supply of good feeding heather. As a rule there is sufficient wind with the snowfall to ensure that large tracts of ground remain uncovered on exposed ridges, and on the weather side of hill faces. When this is so, the Grouse collect on them ; but as these exposed tracts are always on the weather side, and almost always on the shoulder of a hill, it is usually the worst heather which is exposed. The lee side is probably buried deep in snow.

¹ "Annals of Scottish Natural History," vol. vii. p. 27.

² Chap. xix. pp. 414 *et seq.*

Attention has already been drawn to the benefit derived from sheep and deer in time of snow, owing to the surface of the snow being broken by their tracks. But although the heather may be exposed, and even though oats and corn may have been put down in abundance for the birds, the most important step has often not been taken to relieve the necessities of starving Grouse. They must have grit, for without grit it is almost useless to put down corn. This was realised and put into practice in the snowstorm of 1881; but only by very few.

Need of
grit in time
of snow.

Corn was put down here and there for the ravenous birds, and though some of it was eaten it was evidently not what they were most eager to obtain. On one moor, at any rate, men were then sent out with shovels, not merely to expose the heather, but to open up the "scrapes" along the road sides all over the moor, and thus to expose fresh grit. Every day new grit was laid open and rotten quartz and sandy rock were broken out, and each day a fresh supply was needed. Grit, therefore, was what the birds were really starving for, and it was the want of it that rendered them incapable of dealing with hard corn or winter heather. With good quartz grit they can deal with almost anything, even the very woody heather that appears above the snow; without grit they will starve. Any one may assure himself of this by examining the winter crop-contents of the white-winged Willow Grouse or "Rype" of Scandinavia—the bird which decorates our poultry shops as "Ptarmigan" in winter. It is quite wonderful to see how excellent is the condition of these birds, living as they do on hard wooden alder twigs and alder buds, woody dwarf willow twigs and old rank heather. Their crop contents are extraordinarily hard and woody and uninviting in appearance, and yet with good quartz grit it is all ground up and utilised.¹

Another cause of death to Grouse is the ravages of birds and beasts of prey.²

Vermin.

Deaths also occur amongst Red Grouse owing to the antagonism which exists between the male birds of Blackgame and Capercailzie, and those of the Red Grouse. The two former have been blamed for the disappearance of Grouse from certain parts of the country. John Colquhoun, speaking of the decrease of Grouse in some districts says: "This may in part be attributed to the advance of cultivation; but I cannot help

Blackgame
and
Capercailzie.

¹ *Vide* also "Experiments on Effect of Grit Starvation," vol. ii. Appendix F

² *Vide* chap. xx. pp. 443 *et seq.*

thinking the Blackgame have a good share in driving off the Grouse, as I know of one instance where the former were killed off, and the latter again returned to their old haunts. I believe it is also more than suspected that the Capercaillie, wherever they are introduced, have a great inclination to dispossess both."¹

The conditions have altered much since this was written. Large tracts of Blackgame country have been drained and put under cultivation; and Capercaillie have in many places again become abundant after a temporary extinction. Planting has become much more general, and the presence of young larches often determines the movements of large numbers of Blackgame.

Corn feeding is a habit which has become general amongst Grouse and Blackgame wherever the lie of the land permits, or the condition of a moor facilitates it. It is often mentioned as an accompaniment, or a cause, ^{Corn feed- ing.} or a forerunner, or a consequence, of "Grouse Disease." The opinion of gamekeepers on the subject is about equally divided; some say that it does the birds more good than harm, and others say exactly the reverse. Some again say that it does them neither good nor harm, and others that it is a sure precursor of disease. Occasionally yet another suggestion is made which appears on the whole to meet a certain proportion of cases, namely, that in certain districts the weaklings alone are to be found upon the stooks and stubbles, or, in other words, that corn feeding is a consequence of sickness, not a cause. Generally speaking, in districts where large packs habitually come upon the stubbles, it is probably because they have insufficient food upon the moors. Grouse when feeding on the stooks are generally not only healthy but wild, until they have filled themselves with corn, when their habitual weariness often seems to leave them. This has long been recognised, and in Adam's "Reminiscences," for example, we find the statement that "Grouse, when they get on the plough are sometimes very stupid."² A case in point occurs in the extraordinary series of deaths from collision in Blackgame which has been described above.³ Something connected with the corn upon which the birds were feeding seems to have been the cause of their incapacity. Corn feeding then is customary with healthy Grouse on some moors much more than on others; but the evidence seems to show that when *sick* birds appear on the cornfields they are there because they are sick—not that they become sick as

¹ John Colquhoun, "Moor and Loch," p. 202, note.

² Adam, "Reminiscences," p. 25.

³ *Vide pp. 158 et seq.*

the effect of having been upon the corn. St John notes that on August 12th, 1847, during a severe epidemic of disease in Morayshire, Grouse were feeding in numbers on unfilled green oats in the small fields near the moor. This, he says, he had never seen before, though he was accustomed to see Grouse flocking to the stubbles in the autumn.¹

Sickly birds found feeding on the stooks were forwarded for examination in 1908, birds seriously diseased with Cobbold's Strongylosis, wasted piners that could hardly fly. These were probably sick birds that had been crowded out from the good feed on the moor by the healthier birds which live there in packs, and only occasionally make a raid upon the corn.

Possibly the stubble fields may become dangerously infected ground if sick birds frequent them even in moderate numbers. They may contaminate with their droppings far more corn than they can eat, and healthy birds may thus run a risk if they make their visits too frequently. Dangers of
corn feed-
ing. It is perhaps in this way that the idea originated that overmuch corn-feeding is a precursor of disease.

The following extracts bear out this view of the matter :—

Macdonald quotes as follows from a pamphlet written by Mr William Colquhoun of Ross-shire in 1858 :—"The Grouse have fed a great deal on the stooks during the disease (1854-1856); and on the stubbles after the corn was stacked; and also in spring on the sown corn. This year (1858) the Grouse did not come to the corn as in former years." (The disease had then quite disappeared.)²

Again Colquhoun says that Grouse thrive in confinement when fed on corn; but allows that their greed for corn increases in disease years. He thinks that possibly they are upset by eating damaged and unwholesome heather, and are driven to stook and stubble for a sufficiency of food.³

Speedy, too, writes as follows :—

"An excessive consumption of corn by the Grouse species, particularly in wet seasons when the harvests are late, has been assigned as a cause of the 'Grouse Disease.'"⁴ But he goes on to say that hand-reared Grouse can live for several years in perfect health without seeing anything but corn; and that whereas on the Dalnaspidal and Rannoch moors the birds were too far from cultivation ever to see corn, yet they suffered badly from disease in 1873.

¹ Charles St John, "Natural History and Sport in Moray," p. 202. Edinburgh: David Douglas, 1882.

² Macdonald, "Grouse Disease," p. 123. William Colquhoun, "Remarks on the Decrease of Grouse and the Grouse Disease," p. 29. Edinburgh: Edmonston and Douglas, 1858.

³ Colquhoun's Pamphlet, p. 30.

⁴ Speedy, "Sport in the Highlands and Lowlands of Scotland," p. 200.

As with theories based on the belief that Grouse feed on frost-bitten heather, so with those that are based on their feeding upon corn, very little actual evidence is brought forward from *post-mortem* examinations to show that they suffer any harm at all from the latter food, or that they ever under any circumstances fill their crops with the former.

In the examination of some score of birds whose crops or gizzards contained traces of corn, only one or two showed any evidence of damage that could be directly attributed to its presence. These cases are more fully discussed in another chapter.¹ Some of the birds were obviously piners that had been sick for a considerable time, and there is no doubt that their visit to the cornfields was to some extent involuntary for the reason that they found themselves unable to hold their own with the packs of healthier birds upon the moor. To some extent also no doubt it would be inevitable because from sheer weakness each flight would tend to bring them nearer to the lower cultivated ground. But this use of cultivated ground as a congregating area for sick birds depends largely upon its position with respect to the moor. If even a few habitations intervene, the Grouse, whether healthy or unhealthy, will hardly ever visit the corn, except under urgent pressure of starvation.

Conditions very conducive to corn feeding exist in parts of southern Perthshire, where the high ground runs in long and comparatively narrow ridges, while the valleys between the ranges of hills contain open areas of farmed arable land right in the very midst of the lower beats of the moors.

For many reasons such low ground, whether farmed or not, must always be to some extent less healthy than the high ground, and the cornfields the least wholesome parts of all. First, because all the weakly birds on the moor tend to leave the high ground for the low, thus turning the stubble fields into concentration centres. Here, too, large packs of healthy birds making raids from the high ground not only themselves foul the lower ground with an excessive amount of loose droppings full of nematode eggs and unhatched larvæ, scoured from them by the irritating corn husks, but also run a great risk of filling themselves with corn which has been fouled by the convalescent, sick, and more permanently diseased occupants, whose droppings are even more abundantly full of nematode eggs than are their own. This is no doubt the point to which Colquhoun refers when he says: "My opinion is that corn is very unwholesome food for Grouse. Let any person examine the

¹ *Vide* chap. iv. pp. 81-82.

droppings of Grouse when fed on corn, and they will find them similar to tar, but rather browner in colour.”¹ Such droppings are not so abnormal as Colquhoun believed, coming as they do direct from the cæca; but they are full of the ova of *Trichostrongylus*, and are thus a menace to the health of other birds frequenting the same feeding grounds.

Low ground such as this in southern Perthshire must thus have a tendency to become thoroughly infested with the eggs and larvæ of threadworms, as well probably as with the eggs and cyst-bearing hosts of the tapeworms. The higher ground on the other hand has a tendency to get rid of these eggs and larvæ by natural drainage at the expense of the lower ground. Every spate must wash down millions of nematode larvæ from the higher to the lower ground, where often there is little natural drainage, and the artificial drainage is inadequate.

Turning now to the dangers and risks attendant upon the natural processes of production and moulting, we find that the exigencies of courtship, mating, and moulting in the male, of moulting, the laying of eggs, and the hatching out and rearing of a brood of chicks in the female, constitute the sequence of a taxation which bears heavily upon the Grouse. It is worth while to look at them in detail to see to what extent each may fairly be burdened with responsibility.

If an inquiry is made into the cock bird's life he will be found engaged in constant vigilance and warfare from the time of pairing, generally about the end of February or March, onwards for a month or two at least. The battles are more bloody and more disastrous to the weaklings than is generally supposed, and many of the half-starved and parasite-infected cocks, the so-called cases of “disease” found dead along the burns, have really been killed in fighting. It is a fact, testified by more than one reliable gamekeeper, that two or more healthy cocks will sometimes set upon and kill a weakling before they settle their own dispute; and of the urgency of their own dispute the following quotation by Macpherson in the Fur and Feather Series affords a good example. He quotes a Perthshire keeper, who “saw two male Grouse engaged in combat, so completely blinded by fury were the birds that they dashed against the wall of a stone building, one of them killing himself with the impetuosity of his flight.”² In the same work

Risks of
reproduction
processes.

Warfare
among
cocks.

¹ Colquhoun's Pamphlet, pp. 29, 30.

² Macpherson, Fur and Feather Series, “The Grouse” p. 32.

Mr Stuart-Wortley writes: "In the pairing season the old warriors come down from the heights, fight with and vanquish the younger ones, and absorb the young hens."¹ Such efforts combine to bring to an end a very large proportion of cock birds which are more or less exhausted after the winter by poor feeding and the loss of strength due to the presence of intestinal parasites.

Then follows the moult, an exhausting process under the best conditions, and one for which nature generally makes provision by laying in a stock of subcutaneous fat. All this is consumed during the growth of the new feathers.

But in the case of an ill-conditioned Grouse the moult commences with an insufficient supply of fat from which to draw for the growth of the new feathers. The result may be a complete failure to rise to the occasion; or, if the failure be only partial the old feathers will be retained to some extent, and the new feathers will come slowly, poorly, and sparsely. Bare legs and a poor-looking mixture of old and faded feathers, with a more richly coloured new one here and there, produce a seedy, chequered-looking bird, and to this must be added an air of exhaustion and *malaise*. Occasionally in the male the summer change of plumage is not completed even by autumn, and feathers of three different plumages may then be found on a single individual. But as the season advances, and good food becomes more abundant, by degrees the moult is completed in a more or less satisfactory manner. The chief troubles are then over for the cock, and he gradually improves in condition to meet the ensuing winter.

But now to consider the hen, whose lot is certainly less enviable than that of her mate. She also may have struggled through the winter, and while the cocks fight over her is quickly putting on fat for an early moult. She makes an almost complete change of plumage before laying her eggs in April; and in this she must consume a portion of her strength. She recuperates in sitting, but feeds only scantily the while. Then her troubles begin to be more pressing, especially if by any mishap she loses her eggs and has to lay and sit a second time. If, however, by the end of June she hatches off, she must still be constantly on the watch for danger to her chicks. In July she has to moult again. Little wonder that by August she is sometimes reduced to the condition of a "piner," or that, when the shooting season comes, she is discarded from the day's bag, to be submitted for examination under suspicion of "disease."

It is the same story precisely as in the case of birds handicapped for life

¹ Macpherson, Fur and Feather Series, "The Grouse," p. 147.

through having been hatched late in a second brood. In the one case the birds are full grown and healthy to begin with, but have been unable to stand the strain of breeding and moulting. In the other case they have never had a chance to become full grown. In either case the course of natural taxation is the same, the parasitic infestation is the same, and the final result to the bird is the same. The only thing which differs is the primary cause of weakness, and this may be one, or several, of a very considerable number that lie in wait for the life of the Red Grouse on every moor.

Of accidents which may happen in the process of laying, there is one which is well known in captive birds, but must be rare in nature, namely, a shortage of lime rendering the eggs deficient in shell. Soft-shelled eggs not only fail to stimulate the muscles of the oviduct, but ^{"Soft shell."} give them no purchase upon which to act. The consequence is that the egg is not expelled, but is broken in the duct, and is followed by other eggs until the bird dies either from exhaustion or from a rupture of the oviduct involving the peritoneum. Soft-shelled eggs in wild birds generally appear in a second clutch laid shortly after the loss of the first nestful.

Gastro-uterine gestation must always be rare, but one well-marked case in a Grouse was sent up for examination. The egg, when shed by the ovary, failed to enter the open upper end of the Fallopian tube, and so passed into the body cavity. By causing irritation there it became adherent to the peritoneal covering of three portions of the gut. The adhesions formed a firm support, and presumably the egg was for a short time carried safely. Eventually, however, it was broken in the peritoneal cavity, and the bird was shot, and owing to her unwillingness to take flight was forwarded as a case of suspected disease. ^{Gastro-uterine gestation.}

Disease of the skin is a very rare thing in wild Grouse, and generally results from the irritation produced by innumerable ectozoa, ^{Diseases of the skin.} such as ticks and lice.

No. 1634 was an adult hen Grouse of 20 ounces, shot on August 12th, 1908 in Lanarkshire. The bird was very unprepossessing in appearance, as the feathers had failed to make their way through the skin of the head and neck especially, and to some extent all over the body. The skin was of a very deep yellow colour, and there were sebaceous cysts of varying sizes scattered all over the bird, and so thick on the head and neck that hardly a feather appeared. The gamekeeper's view was that it looked "like a hen that

had sat herself out on frosted eggs." There was no other abnormality discovered except the large size of the spleen which measured 20 mm. in length and 11 mm. in thickness.

It is difficult to give any reason for this occurrence of sebaceous cystic disease of the skin. No other case of the kind has been brought to the notice of the Committee. It is somewhat analogous to acne, and it may possibly have been preceded by an eczematous irritation of the skin brought about by *Ixodes*, the Grouse tick; it resulted in any case in the failure of feather growth and disease of the glands which should have assisted in the process.

The only other case which resembled it somewhat was Grouse No. 1792, where *Ixodes* and *Goniodes* had again produced a great number of scabs and sores and warty excrescences all over the face and head, and especially in the neighbourhood of the ears and eyes.

CHAPTER IX

"GROUSE DISEASE"

History of "Grouse Disease" with an account of the work of the "Grouse Disease" Inquiry, in respect of previous work done by Professor Klein, Dr Cobbold, and others.

By Edward A. Wilson and A. S. Leslie

"GROUSE Disease" in its epidemic¹ form has become a serious matter only since the Grouse has come to be of importance in the economic management of estates in England and Scotland.

Careful protection, improved conditions of food caused by heather-burning and drainage, and the removal, as far as practicable, of all animals that seriously affect the increase of the birds, are some of the artificial means by which moors have become more heavily stocked with Red Grouse than was the case under more natural conditions. To this heavy stocking, combined sometimes with unfortunate natural conditions, but oftener with injudicious management, have been attributed the outbreaks of epidemic disease which have periodically visited the majority of Grouse moors. In other words "Grouse Disease" has always been considered to be intensified by artificial conditions.

It is doubtful whether this view is correct; as early as the end of the eighteenth century we have records of serious mortality amongst the Grouse in certain districts, and "Grouse Disease" undoubtedly occurred in the earlier part of the last century, long before the artificial conditions had become established.

It is therefore probably not correct to say that the first predisposing cause of "Grouse Disease" was protection leading to overstocking. The question is really

¹ The familiar word "epidemic" is used throughout these volumes to signify outbreaks of specific diseases among Grouse in place of the more correct term "epizootic."

of academic interest, since the artificial conditions are now firmly established, and it might be profitable to consider the other theories which have been put forward as to the predisposing causes of disease.

Predisposing causes of "Grouse Disease." Such theories are numerous, and every one of them has at one time or another been promoted to the rank of "the real cause," the acting and primary cause, that is to say, of so-called "Grouse Disease."

Before discussing their relative importance, however, it will be well to mention shortly what is known of the earliest appearance of the disease, and of its distribution in time and space.

Among the earliest recorded outbreaks of disease about the beginning of last century, Macdonald, in "Grouse Disease," says: "It is now (1883) eighty years since the alarm of 'Grouse Disease' was sounded in this country."¹

Speedy says: "The first time 'Grouse Disease' attracted special attention was in 1838. Prior to that date it was not unknown in Scotland; but it had not assumed the proportions of a malignant epidemic.

"Even in 1838 and for several years afterwards, it was much milder in its results than it has latterly become. In 1867 it seems to have developed a most destructive form, attracting very general attention. Prior to that it was comparatively local, decimating the birds in certain districts, and leaving other districts untouched."²

Howard Saunders says: "As long ago as 1815 a severe outbreak in the Reay country, Sutherland, was on record."³

Mr Woodruffe Peacock in a pamphlet on "Grouse Disease" writes: "Old Moor Keepers have told me that their elders knew it as a slight and local trouble quite 50 years before 1847," i.e., in 1797.⁴ And finally, in the MS. Records of Bolton Abbey, it is specifically mentioned as a "fatal disorder" in 1822; though as early as 1809 and 1811 there are records of "no shooting"—accountable in all probability to disease.

Distribution of "Grouse Disease." Of the distribution of "Grouse Disease" in space it is more difficult to speak shortly, and the question deserves very close consideration. Not very much had been made of the subject up to the time of the commencement of the present Inquiry. It may be of use, however, to give an idea of the lines upon which the Committee has been working.

¹ Macdonald, "Grouse Disease," p. 112.

² "Sport in the Highlands and Lowlands of Scotland," p. 184.

³ "Zoologist", 1887, p. 302.

⁴ Rev. E. A. Woodruffe Peacock, "Grouse Disease," p. 12.

An attempt has been made to work out the distribution of disease in Grouse, both in time and in space, by first collecting records from every possible source, and as far back in time as it is possible to go. Each record is then allocated to its proper position on a map for its own proper year. By having a separate outline map of the British Isles for each year, on which every outbreak and every occurrence of disease is marked in red, it is possible at a glance to arrive at certain conclusions, *e.g.* :—

1. How the incidence of disease changes from one set of counties or one district in one year to another set of counties or to another district in the next year; thus the track of the epidemic from year to year can be distinctly followed.

2. The frequency of disease in each district is seen at a glance, and its rise and fall during the years which intervene between the periodic outbreaks can be followed.

3. The disease-incidence of each year can be compared with its weather record, and conclusions thus may be drawn regarding the predisposing causes, as well as the method of dissemination.

4. By combining a large series of annual disease-records on one map an idea is obtained as to which areas suffered most, and whether any areas are disease-free.

5. Such a combination of annual disease-record maps can be superimposed upon similar maps showing rainfall, watersheds, heights above sea-level, and surface soils or sub-soils, and so it becomes possible to recognise whether disease is in any way connected with one or other set of physical conditions.¹

"Grouse Disease" has long held the attention of many observers. Sportsmen and naturalists have done much for the field work, but the laboratory work has been less popular. Klein, Cobbold, Farquharson, Colquhoun, ^{Previous} Andrew Wilson, and Young have all contributed towards an under- ^{work done} ^{on "Grouse} standing of the pathology of "Grouse Disease," while Macdonald, ^{Disease."} Macpherson, Stuart-Wortley, Adams, Speedy, Teasdale-Buckell, and a host of other naturalists and sportsmen have supplied a large collection of interesting facts and observations, and an almost equal number of hypotheses and theories to account for them. It will be of use first to discuss the conclusions at which various writers have arrived, and as Klein's work stands out pre-eminently, and includes so great a proportion of what was known about "Grouse Disease" at the time, the simplest course will be to take his conclusions first.

¹ For the results of this branch of the Inquiry, *vide* vol. ii. Appendix I.

Professor Klein came to the conclusion that there was a disease amongst Grouse which took the form of an acute infectious pneumonia, and was characterised by the presence in the lung of a specific bacillus of the *B. coli* group.

The disease had, he believed, two classes of victims, one which died rapidly in plump condition and fine plumage, and another which died slowly with emaciation.

He puts on one side the whole question of parasitic intestinal worms as having no particular connection with this epidemic pneumonia, and no causal connection with the mortality. Further, he agrees with the views of Dr D. G. F. Macdonald, and allows that Dr R. Farquharson was the first (in a letter to the *Lancet*, September 1874) "to state the opinion that the 'Grouse Disease' was of the nature of a contagious fever."

Dr Farquharson's view as given in Macdonald's "Grouse Disease," was that the malady resembled an infectious or contagious epidemic fever. He considered that the finding of dead birds, "some plump and in good condition, and some reduced to skeletons," was in favour of the view "that the disease is of a specific or constitutional nature."¹

Klein disagreed with Dr T. Spencer Cobbold's view that the epidemic "Grouse Disease" was due wholly to the presence of nematode worms.

Dr Cobbold's view, was that "in the present epidemic" (1872), the disease was "entirely due to parasites," and that "the occurrence of these parasites in

the intestines of so-called healthy Grouse does not destroy the notion of disease from this source." "A strong bird," he says, "will overcome or

resist the irritation set up by the presence of hundreds of entozoa; while a feeble bird, or one attacked before it is perfectly grown, will more or less rapidly succumb to the invasion. On these and other grounds, therefore, I do not hesitate to express the opinion that the present Grouse murrain is due to parasites. The irritation, probable distress and subsequent emaciation of the birds are readily explained by the presence of hundreds and thousands of strongyles; and the mere circumstance that these parasites are very small, is quite sufficient to account for the fact that investigators have hitherto overlooked them."²

"In one extreme case," he continues, "I particularly noticed a remarkable gorged or distended condition of the cæcal villi, such as would result from continual irritation set up by parasites in overwhelming numbers. . . . There

¹ Macdonald, "Grouse Disease," p. 129.

² T. Spencer Cobbold, M.D., F.L.S., F.R.S. "The Grouse Disease," p. 15. London: The *Field* Office, 1873.

was no rupture of the capillaries, and consequently no extravasation in the cæca or in any part of the intestinal canal. That this congested state of the villi was due to the strongyles appeared the more certain, since the turgidity was only marked in that part of the cæcum where the strongyles were crowded together."¹

Dr Cobbold considered that the difference observed in the intensity of the disease during various epidemics might be partly accounted for by the presence of tapeworms and threadworms in varying proportions in the same Grouse, but that the strongyles were "sufficient by themselves to cause the death of the host" without the "assistance of a second kind of parasite."²

Klein too recognised, not so much a different type of disease in different years, as two distinct phases of the same disease in the same epidemic, namely, that which is so acute as to kill birds in good condition without giving them time to lose flesh, and that which is so much less acute that it gives its victims abundant time to become emaciated before death.

Cobbold, however, differed from Klein in one important respect, viz.:—that he distinctly indicates that he did not observe any example of a Grouse dying in good condition and without loss of flesh.

Neither Klein nor Cobbold suggest that they had any suspicion that they were dealing with two distinct diseases.

Taking all these facts and opinions into consideration, the Committee at an early period adopted the provisional view that Klein and Cobbold had before them Grouse dead from two distinct diseases—(1) plump and well-conditioned birds which had died of an acute infectious pneumonia, *i.e.*, the acute form of Klein's "Grouse Disease"; and (2) emaciated piners which had died of the results of extreme parasitism, *i.e.*, of Cobbold's Strongylosis. The Committee kept in view, however, that since there is no reason why a bird already dying of Cobbold's Strongylosis should not become infected with, and succumb to, Klein's infectious pneumonia, it was possible that the piners examined by Klein might also be cases of the acute infectious pneumonia, which had stepped in and made an end of their already diseased existence.

Com-
mittee's
provisional
view—two
distinct
diseases.

Endeavour
to reconcile
Klein's
views with
Cobbold's
views.

It would have been obvious to Dr Cobbold, if he had ever really seen a clear case of a Grouse which had died in good condition, well up to average weight, but with pneumonic lungs, that its death must have been due to some more acute cause than the mere presence of nematodes in the gut.

¹ Cobbold, "Grouse Disease," pp. 24, 25.

² *Ibid.*

It was clear that Dr Cobbold's experience had lain entirely with emaciated birds, while Professor Klein as we know observed birds of all kinds; but always from moors where the pneumonic disease appeared to be rampant.

It had been generally noticed in past epidemics of disease that the first victims were of the emaciated type. It was only in the later stages of the outbreak that birds in apparently robust health were said to have been found dead often "sitting on their nests."

The Committee believed it not unlikely, judging only from the limited evidence before them, that the reason of this was that the acute pneumonic disease picked out first and made a clean sweep of birds already emaciated by Cobbold's Strongylosis. These piners would naturally be concentrated on the lower ground, and since their power of resistance to disease would be low any infection would naturally spread rapidly amongst them, while the more healthy birds on the higher beats, with a greater disease-resisting power in them, would be less prone to take the infection immediately, and also would be less readily discovered on the higher ground, even when the disease had proved fatal.

This hypothesis appeared to account for a clean sweep of the piners all over the moor, and for the distribution of their bodies in large numbers along the burn-sides, before the disease could reach the healthy Grouse on the upper ground, or at least before the dead bodies of Grouse on the high ground were discovered in any number.

There appeared therefore in the early days of the Inquiry to be some reason for suspecting that both Klein and Cobbold had confused two separate diseases under the common title "Grouse Disease."

And with regard to this point the Committee were probably in a better position to judge than those who had preceded them, in that the latter had begun and ended their work amongst innumerable dead and dying Grouse, the victims of a chronic wasting form of disease, often, it seemed, inseparably mixed up with the victims of a widespread epidemic of acute pneumonia.

One thing was quite certain, that whereas the Committee had seen during the first three years of the Inquiry extensive mortality amongst Grouse caused by some agent which acted slowly and produced "piners" only, they had not seen anything at all like an epidemic of acute or infectious pneumonia. It followed therefore that if the rapid

Character
of past epi-
demics.

Might be
accounted
for by both
Klein's and
Cobbold's
theories.

Only one
form of
disease
observed
by Com-
mittee.

death of birds in good condition was typical of Klein's disease no case of Klein's disease had yet been seen.

At this date the only form of disease observed was a very widespread mortality of "piners" owing to what appeared to be a form of starvation resulting from a chronic congestion of the cæcal mucosa. This condition of the mucosa was produced by an excessive number of the nematode worm known as *Trichostrongylus pergracilis* in the cæca, and was quite comparable to the form of "Grouse Disease" described by Cobbold.

Character
of disease
observed
by Com-
mittee.

The view that two distinct forms of disease had for many years past been confused under one term was supported by the literature of the subject, for all previous writers on Grouse and "Grouse Disease" had referred to a difference in character to be noticed between the disease outbreak of one year and that of another, or between the appearance of the victims at one season and another in the same epidemic.

Committee's
view sup-
ported by
the litera-
ture.

By adopting the view that two distinct diseases had been confused, much of the disagreement which had been in evidence from the earliest days, as to the predisposing causes of "Grouse Disease," could be explained.

The following abstracts suggest that there were two different agencies at work destroying Grouse in large numbers.

William Houstoun of Kintradwell, Brora, for instance, says: "At that time it took the tapeworm type, and the birds all came down to the seashore to pick up particles of salt; but, when the disease next appeared, it had a different form, and I fear we are as far as ever from a solution of the cause. I opened three birds in the last stages of the disease" (the pining form) "and they all presented the same appearance. The liver like a clot of coagulated ink; intestines distended with a yellow feculent matter; and crop full of undigested but fresh and green heather tops."¹

These were presumably cases of Cobbold's Strongylosis, since the distension of the intestines "with a yellow feculent matter" suggests the appearance characterising the cæca in that disease, and the victims were all piners.

Again, Macdonald, in his book on "Grouse Disease," described the earlier stages of the epidemic as being much more virulent, the birds being found dead and dying in numbers by the water-courses, "which latterly was not the case." The plumage in the earlier attacks looked different, the feathers were dirty

¹ Macdonald, "Grouse Disease," p. 140.

and dragged — an appearance which was “latterly not seen in diseased birds.”¹

And again, quoting from “Land and Water” (1867), he says that “one striking difference between the disease of 1867 and that of former years was that the dead birds . . . picked up this season were so plump and in such excellent plumage that they had the appearance of healthy birds; whereas in former years the diseased birds were most characterised by disordered plumage and attenuated bodies.”²

From this the Committee surmised that the disease which occurred in 1867 was Klein’s pneumonia; while in the previous records the birds had been victims of Cobbold’s Strongylosis. This provisional view was again borne out, by a letter written by Mr Macdonald to the *Times*, May 12th, 1873, which ran thus: “It seems that disease of an exceedingly virulent kind prevails in all parts of the Highlands, and in a form hitherto unknown. . . . In 1847, 1856, and 1865 the infected Grouse exhibited a ‘dull disordered plumage and attenuated bodies.’ . . . In June 1867 they showed good plumage, a healthy appearance, and were perfectly plump, although the liver was soft and discoloured. This year (1873) they are beautiful in plumage, but wasted to skeletons . . . and with full crops.”³ This occurred evidently in later autumn, since mention is made of the large quantities of berries in their crops.

All these quotations seemed to point to the fact that in 1856 and 1865 there was an excessive mortality from Cobbold’s Strongylosis; whereas in 1867 there was an epidemic of Klein’s acute infectious pneumonia.

In 1873, the birds which were seen late in autumn were presumably recovering, thanks to a full diet of berries, or, if found dead, were to be considered cases of Cobbold’s Strongylosis killed by Klein’s pneumonia. They may have survived an attack of acute pneumonia which the Committee were prepared to believe had raged that year, but they certainly were also victims of Cobbold’s Strongylosis; and the fact that their plumage was in good order seemed to show that they were at any rate sufficiently convalescent to complete the growth of their winter plumage after moulting.

Macdonald writes: “We have ourselves frequently picked up dead Grouse perfectly plump, and in excellent plumage one season, and in the next season found diseased birds with attenuated bodies and dull disordered plumage.”⁴

¹ Macdonald, “Grouse Disease,” p. 127.

² *Ibid.*, p. 155.

³ *Ibid.*, p. 155.

Ibid., p. 131.

Again, in Adam's "Reminiscences" we find: "Disease in this attack (Dalnawillan, 1882) was very different in its aspects from former attacks. It came on very suddenly, sharp and decisive; but on this occasion I have no doubt but that it had been hanging about all through 1881, and also in the spring and summer of 1882, steadily wearing away the birds bit by bit."¹ The distinction is markedly contrasted by Adams in his book, and the incidence in each case is well described.

Tom Speedy in "Sport in the Highlands and Lowlands of Scotland" writes: "The epidemic assumed two different forms. In some cases the birds were dragged, wasted, and emaciated, bare about the legs, and indicating . . . a long continued or fatal disease. At a more advanced period of the season they were found dead in beautiful plumage, with fine feathery legs; and the red above their eyes unsullied and as bright as vermilion. In many cases they were seen the one day seemingly in perfect health, and the next day stiff and cold in excellent condition."²

Enough has now been quoted to show that in the minds of many observers there has been for years the suspicion that the differences observed were not merely two phases of one form of sickness, but two distinct diseases. And it was on this assumption that the Committee at first commenced their investigation.

The widespread idea that tapeworms are at the root of one form of trouble is perhaps natural, considering that it is common knowledge that in some animals they are the cause of serious wasting. Moreover, the very first thing that appears when a Grouse is opened up, whether purposely or accidentally, is a mass of large white tapeworms. What could be more natural, since the bird is wasted to skin and bone, and tapeworms are found in large numbers, than to consider the one to be the cause of the other. But if only threadworms were as conspicuous as tapeworms, outnumbering them as they often do, to an almost incredible extent; or if some distinction had been earlier recognised between the main gut of the Grouse and its cæcal appendices, there would before now have been a strong following of Dr Cobbold, and the pining form of disease would be more readily associated with the presence of the smaller worm.

The Committee's provisional belief in the existence of two distinct kinds of

¹ Adam, "Reminiscences," p. 75.

² *Op. cit.*, p. 185.

No case of Klein's disease yet observed. "Grouse Disease" appeared to be justified up to a certain point, but as there has as yet been no outbreak of Klein's epidemic pneumonia within the Committee's knowledge, it was impossible to speak positively upon the subject.

Klein, of course, had "piners" to work with as well as "birds that died in good condition" before they had time to pine; but as already stated he came to the conclusion that they exemplified two phases of the one disease.

It appeared quite reasonable to believe that in an epidemic of the infectious pneumonia some of the birds might survive long enough to become piners; therefore the Committee were prepared to accept Klein's explanation in so far as it applied to the birds which he had the opportunity of examining. But it could never happen that uncomplicated cases of Cobbold's Strongylosis should die plump and in good condition.

Loss of weight an invariable accompaniment of Cobbold's disease. All birds dying from Strongylosis must be "piners," because their death results mainly from an inability to absorb nourishment owing to the cæcal mucosa being damaged. The consequent emaciation is a *sine quâ non* in the diagnosis.

The weak point, as it appeared to the Committee, in Klein's argument was that he makes no adequate mention of the cæcal lesions caused by the *Trichostrongylus*, lesions which in the majority of adult birds examined by the Committee have been the most prominent, indeed the only prominent feature upon dissection, and which the Committee believe to be at the root of the whole question.

Before proceeding further to discuss this point it will be well to look into the accounts of dissections which have been recorded from time to time (many unfortunately in the most cursory manner), with a view to seeing what pathological lesions were found to account for death.

Klein's work is again in many respects far ahead of all the rest; and as it is necessary to go into it in some detail it will be better first to glance at the work of others.

Dr Cobbold's notes on the pathology of "Grouse Disease" have already been quoted;¹ but reference must again be made to a description which he gives of the cæca in an "extreme case" dissected by him.

¹ See p. 188.

"In one extreme case," he says, "I particularly noticed a remarkably gorged or distended condition of the cæcal villi, such as would result from continual irritation set up by parasites in overwhelming numbers. . . . There was no rupture of the capillaries and consequently no extravasation in the cæca or in any part of the intestinal canal."

This condition of the cæcal villi is very typical of extreme Strongylosis as observed by the Committee, just as the same engorged condition to a lesser degree of the intestinal villi is typical of Helminthiasis generally. Nor is it by any means so rare as one might gather from Cobbold's description. Yet Professor Klein makes no mention of any condition at all approaching it in character, in any of the birds examined by him, though he allows the almost universal infection by the *Trichostrongylus*.

Professor John Young wrote a paper on *Certain Aspects of the Grouse Disease*, in the "Natural History Proceedings of the Glasgow University," vol. i. (quoted in Macdonald's "Grouse Disease").¹ Unfortunately, he does not differentiate between the different portions of the intestine; but he appears to have had a most abnormal series of birds to examine. In two of three Argyllshire birds he found general peritonitis due to perforation of the gut which must have occurred a sufficient length of time before death to allow of adhesion and short circuiting.

Dr Andrew Wilson is also represented as having satisfied himself "by repeated dissections and careful observation that a markedly congested appearance of the mucous surface and of the digestive and respiratory tracts was almost invariably present in birds which had been found dead."²

John Keast Lord and Frank Buckland are represented by the same indefatigable collater as having "satisfied themselves that the disease was dis-organisation of the liver accompanied by inflammation of the chest viscera." The pity is that we can never know what amount of exact observation these vague descriptions really covered. As they stand they cannot be considered of any value.

Tom Speedy writes as follows rather more to the point: "In *post-mortem* examination in a number of birds we discovered intense inflammation of the bowels; while by the aid of the microscope, immense quantities of strongyle were discernible in the inflamed parts . . . such cases were exceptional when contrasted with that other more loathsome form of the malady which seems

¹ Macdonald, "Grouse Disease," p. 141.

² *Ibid.*, p. 145.

Pro-
fessor J.
Young.

John
K. Lord
and F.
Buckland.

Tom
Speedy.

to have been much more contagious.”¹ By “the other” more loathsome form of the malady he meant the acute disease which killed off birds while still in excellent condition; and, it is interesting to note, that, during this epidemic, cases of “Cobbold’s Strongylosis,” such as he first described, were apparently exceptional.

It is easy to see how incompatible was much of this with what the Committee had seen of “Grouse Disease” during the first few years of the Inquiry, during which “Cobbold’s Strongylosis” had been in many places abundant, and Klein’s acute infectious pneumonia had been not only exceptional, but non-existent.

Turning now to Klein’s account of the pathology of “Grouse Disease,” and remembering that he considered both the piners and the birds that died in good condition as alike victims of an acute infectious pneumonia, we find Klein, a very definite statement of pathological signs and lesions which he diagnosed as the acute pneumonic disease.

“One of the most prominent pathological changes in the diseased Grouse is an acute congestion of one or both lungs, and this change, whether very severe or less severe, is independent of the presence of Strongylus.”²

This implied absence of Strongylus is difficult to accept as a fact, notwithstanding Professor Klein’s statement and the general accuracy of his observations.

The Strongylus is almost universally present in the Red Grouse of all ages, as the Committee has been able to ascertain by the examination of some two thousand birds from every part of the United Kingdom. When-
Strongylus
almost uni-
versal in
Grouse.
ever a case occurred in which its presence was not at once evident, a special search has almost invariably revealed it.

Dr Andrew Wilson came nearer to the truth of this matter when he stated that “in one or two doubtful instances only could it be asserted or suggested that none of the round worms were present.” He nevertheless puts
Dr Andrew
Wilson.
Helminthiasis aside, and believes that the “Grouse Disease” is in the main an infectious fever. He does this, moreover, with every show of good reason, and in words to which we can hardly take the smallest exception, save that he makes too light of the trouble which we now call Strongylosis. He says, for example: “Outside the parasitic hypothesis, applicable as that theory is to a certain class of cases, there lies, I am convinced, the great bulk of fatal instances, the exact cause of which fatality must be sought for in some lesion analogous to that involved in the idea of the epidemic theory.”³

¹ Speedy, “Sport in the Highlands and Lowlands of Scotland,” p. 185.

² Klein, “Grouse Disease,” p. 6.

³ Macdonald, “Grouse Disease,” p. 148.

He was handicapped by this belief in the epidemic theory, but we have to confess that it is difficult to accommodate his observations to the belief in Strongylosis, for he says that there was an "absence, *in most cases*, of the signs of fatal parasitism, such as inanition producing the pining condition, actual perforation, morbid appearance of the muscular tissues, etc."¹

For if most of the cases that he examined were marked by an absence of inanition, they differed very materially indeed from all the cases of birds found dead or dying within the years of the present Inquiry; almost all of which were "piners" to a greater or less degree. But, like all other early writers, he produces no particulars as to weights, and in the absence of these it is impossible to accept as a fact that inanition was absent, knowing as we now do, how exceedingly misleading are the external appearances of many of these cases.

Former writers kept no record of weights.

Klein did not believe in two distinct diseases, and described the autumn and winter cases as having pathological appearances identical with those found in the unwasted Grouse which had died of disease during the spring and early summer. He believed these autumn and winter victims to be sporadic cases of "the real Grouse Disease," which occurs in the spring and early summer. Nowhere throughout his whole book can any suggestion be found that goes even so far as Dr Andrew Wilson's view, that a few birds at least may succumb to Strongylosis, or even to general Helminthiasis.

Klein did not recognise two distinct diseases.

Klein appears to include all the Grouse which he described with the appearance of a pneumonic lesion in the lung, at any time of the year, as victims of the true "Grouse Disease," and by this he meant in every case the acute infectious pneumonia which he was the first to describe in detail, but which the Committee now believes has no existence, and was founded on a misinterpretation of *post-mortem* changes in the dead bird.

What then were the appearances upon which he relied in making a diagnosis of acute infectious pneumonia?

He sums them up once or twice on pp. 15-19 of his book on "Grouse Disease."

The points on which Klein based his theories.

"The chief changes are undoubtedly those found in the lungs.

"(α) In emaciated birds the disease of the lungs is, as a rule, but not without exception, not very extensive, only a portion of one or both lungs being congested.

¹ Macdonald, "Grouse Disease," p. 148.

“(b) In the majority of instances in which the dead birds are found plump . . . the lungs show a great deal of congestion.

“The lungs show deep coloration in the greater part of either one or both organs, the hind portions being, in these cases, the ones chiefly affected ; or both lungs are uniformly congested, being in some cases of a dark purple-red colour.”¹

On microscopic examination of the lung, Klein finds “that in the congested parts the large and small vessels are uniformly distended and filled with blood, and that the air spaces of the more deeply affected parts are uniformly distended and filled with a homogeneous or granular exudation, or with blood, so that in these parts we have a solidification of the lung which compares with the condition known as the red hepatisation in pneumonia. There is, however, no fibrine in the form of threads noticeable in the air spaces ; the smaller air spaces contain blood *en masse*, while the large ones are filled with a homogeneous albuminous exudation. From this we conclude that rupture of small vessels had taken place during life.”²

To continue further with the pathological signs to which Klein has drawn attention, “the larynx and trachea,” he says, “exhibit a change in the mucous membrane, which is of a dark colour, and hyperæmic, and this is the more pronounced the more marked the lung-change. The spleen is not enlarged, and appears of a dark colour.

“The liver is uniformly congested and soft ; it is either of a dark red colour, or appears almost black. On microscopic examination the large blood-vessels as well as the capillaries of the lobules are distended and filled with blood corpuscles. In some cases the liver, on *post-mortem* examination, is blackish, or rather is of a dark olive-green colour. In these instances the liver cells appear granular and more or less disintegrating, and contain dark brown pigment granules, while the capillary blood-vessels are filled, not with blood corpuscles, but with masses of amorphous pigment, the result of stasis and disintegration of the blood corpuscles.

“The kidneys are congested, in some instances leading to hæmorrhage into the tissue of the kidney.

“The intestinal mucous membrane shows patchy congestion, and the same is the case with its serous covering, which in most instances is congested in many places, sometimes to a considerable extent. In some cases the peritoneum appears very moist in these localities ; that is to say, there is a small amount of exudation.

¹ Klein, “Grouse Disease,” p. 15.

² *Ibid.*, p. 17.

"I have seen a few cases in which hæmorrhage has taken place, showing itself in the form of petechiæ in the peritoneum."¹

These appearances which Professor Klein believed to be diagnostic of the acute infectious pneumonia are summarised on page 44 of his book, as follows:—

"The congestion of one or both lungs, the congestion of the liver, the small dark spleen, and the patchy redness of the intestine and the peritoneum," and one may add, the presence of the specific bacillus in the lung and liver of affected birds.

Although the bacillus is not present in the circulating blood of birds affected during the spring and early summer outbreaks, appearing then mainly in the lungs and liver, they are to be found, he tells us, in the circulating blood of birds that have died in the autumn and winter. He believes, moreover, that the latter are the sporadic cases which keep the disease lingering through the winter, ready to break out in a spring or summer epidemic, though the vitality of the microbe is such that it probably requires no such active assistance from individual birds.

Presence
of bacillus
in blood.

It will be seen that it appeared impossible for the Committee to accept unconditionally the views of any of their predecessors in the work; but it seemed equally impossible to discredit altogether the reliability of detailed observations made by many workers of high standing. At this stage of their investigation the Committee still believed that Klein's "Grouse Disease" was an established fact (though his diagnosis might require revision), and spoke of it as the "true epidemic Grouse Disease," or "Klein's acute infectious pneumonia."

At the same time, the Committee believed it to be an advantage for them to see one disease at a time, and began to distinguish Cobbold's Strongylosis as a specific disease apart from Klein's acute infectious pneumonia.

The foregoing *résumé* is necessary in order to show the position of the controversy when the Committee of Inquiry was beginning its work. It explains many of the unavoidable errors into which the Committee was led by the inaccuracy of much that had been published on the subject. Even Professor Klein's work, accurate and painstaking as it was, and clear as were his published descriptions of whatever he himself saw, was misinterpreted by him for the sole reason that bacteriology (a science of which he was one of the most honoured founders) was still in its infancy. His deductions as to the disease being an acute infectious pneumonia due to a specific bacillus have now been shown to be founded upon a misconception;

Cause of
Professor
Klein's
error.

¹ Klein, "Grouse Disease," p. 19.

but, in the days when he was working at the subject, no one could have arrived at other conclusions than those to which he himself came. It is due to so great and careful a worker to say that at that time he was years ahead of any other bacteriologist. That he should since have been found to be in error merely shows how dependent is science upon the methods available at the moment, and how impossible it is for any one at any time to be certain that even the most probable explanation of observed facts is the right one.

It has been thought necessary to set forth the different stages of opinion through which the Committee has passed in order to account for many provisional conjectures, since shown to be faulty, as to the cause of death in birds that were submitted for examination in the earlier days of the Inquiry.

Com-
mittee's
early
diagnoses
incorrect.

From the first it was thought advisable to acknowledge the receipt of every bird sent to the officials conducting the Inquiry, and, where possible, to account for its death or its sickness, or for any abnormality which it presented.

In the earlier days the field-observers believed firmly in Klein's view that "Grouse Disease" was an acute infectious pneumonia, and in a few isolated cases they believed that the lesions described by him with so much detail were present. They thereupon made the necessary diagnosis and sent in their report, and for the next week or two awaited an inundation of dead birds showing similar lesions. But no epidemic occurred and the inundation did not happen, and by degrees it became evident that there was something doubtful about the view which had been provisionally adopted.

This doubt was confirmed when the bacteriologist, Dr Seligmann, found that the bacillus which Professor Klein considered to be the specific cause of Grouse pneumonia was in fact only to be discovered in any number some twelve or twenty-four hours after death. It became gradually clear that not only the grosser appearances in the lung which Klein considered to be due to pneumonic congestion, but the microscopic appearances of the lung-tissue in section, as well as the colonies of bacilli which he described and figured in the lung, were in fact only to be found some hours or days after the death of the bird. They were undoubtedly due to a *post-mortem* migration into, and colonisation of, the tissues in question by numbers of *Bacillus coli* which had escaped from their proper sphere in the intestine at the moment when the normal defence had broken down.

Klein's
bacillus
found to be
due to *post-
mortem*
change.

It gradually began to dawn upon the Committee that the appearances in

the lung upon which Klein had relied in making a diagnosis of acute infectious pneumonia differed in no way from the appearances which had been observed by the Committee in the lungs of hundreds of birds found dead from all causes, including Cobbold's Strongylosis, general Helminthiasis, accidents, or even shot wounds.

Similar character-istics found in all dead birds.

Klein describes accurately the *post-mortem* changes leading to a discoloration of the lungs which invariably take place. These begin, almost always, where the lung is in contact with the liver, and strongly suggest (what at first the Committee frequently mistook it for) congestion and pneumonia.

This discovery undermined the faith which the Committee were prepared to place in the existence of Klein's acute infectious pneumonia, and it soon became evident that in birds obviously dying of “Grouse Disease,” there was no dangerous *ante-mortem* infection of the lung or other tissues with the bacillus in question, and no recognisable lesion in any organ of the bird except in parts of the intestine. All the appearance of congestion and pneumonia in the lung, the “inky” or “tarry” appearance of the liver, the small dark spleen and the several other characteristics which were previously attributed to Klein's pneumonic disease, were now found to be due to *post-mortem* change alike evident in diseased and in perfectly healthy normal birds.

The point was further tested by taking a number of healthy pigeons, and killing the whole of them at the same time with chloroform. The birds were numbered and opened on consecutive days and the change in the appearance of the viscera was noted. It was evident that in every case where there had been extravasation of blood or serous fluid owing to rough handling, or damage by the knife in dissecting the pigeon, the tissues of the lung became black, and took upon themselves precisely the same appearance that is seen in a Grouse found dead upon the moor, or examined some days after being shot. The appearance of pneumonia was evidently due to a soaking of the lung-tissue in decomposing blood and serum, and the *post-mortem* colonisation of the tissues by *Bacillus coli*.¹

Experiment upon healthy pigeons.

Once this fact became clear, the Committee was no longer burdened with the task of recognising and investigating the type of “Grouse Disease” described by Professor Klein, for it now became impossible to accept his explanation of the disease. This being recognised it became necessary to set on foot more detailed investigations to determine the following points :—

Points to be investigated by the Committee.

¹ *Vide* also chap. xii. pp. 273 *et seq.*

1. To prove that the amended view of Klein's work was the right one, and that the "Grouse Disease" which he saw and described as a form of infectious pneumonia was in reality not different to the "Grouse Disease" which the Committee were seeing constantly, and were describing as Cobbold's Strongylosis.
2. To make every effort to obtain fresh and living samples of wild Grouse actually suffering from "Grouse Disease," for systematic laboratory work, with a view to discovering whether this or any other widespread form of "Grouse Disease" was caused by bacterial infection or not.
3. To complete the investigation of the Grouse parasites, ectozoa as well as entozoa, with a view to determining whether by any possibility "Grouse Disease" could be considered attributable to some of them, or even to one of them.
4. To investigate the blood of the Grouse in health and in sickness, and especially to try and discover the presence of toxæmia with its resultant anæmia and changes in the respective proportions of leucocytes. It was thought possible that the toxins produced by Helminthes in the intestine might be the cause of some increase in the eosinophil corpuscles.
5. To make certain that "Grouse Disease" did not result from the presence in the intestines, or in the blood, of any protozoan parasite for the transference of which we knew the Grouse had ticks, bird-lice, flies, fleas and other external parasites.
6. To make a complete and special investigation of the life-history of the *Trichostrongylus pergracilis* or the Strongyle of Cobbold, with a view to understanding its mode of infecting Grouse, its action when in the cæcum of the Grouse, its method of reproduction, its dissemination, and the conditions which enable it to hatch from the egg, to pass from the larval stage to encystment, to survive on a Grouse moor, and to ensure its being swallowed by the bird at a stage when to be swallowed means completing the cycle of parasitic life, instead of being merely digested. The life history of this threadworm was obviously required in its smallest details, in order that Strongylosis might be understood.

How these various questions were dealt with may now be explained.

During the period of the Inquiry all the birds that have passed through the Committee's hands, have been examined as carefully as circumstances allowed at the moment. Every bird, almost without exception, was dissected, and the more important points were noted and tabulated, providing in this way a very considerable mass of observations from which to deduce averages, construct tables and curves, and so obtain information which had previously been inaccessible.¹

In addition to this, in the majority of the more interesting cases, parts of the various organs, as well as the contents of the different portions of the alimentary canal, were submitted to microscopic examination. The tissues were hardened and cut, and a very large number of sections examined microscopically, not by one member of the staff alone, but by a number of workers qualified to give an opinion upon what they saw, so that bit by bit a true reading of the observed facts was attained.

One or two questions regarding Professor Klein's work were to some extent settled by the bacteriological work which Dr Seligmann carried out in the first two years of the Inquiry. Dr Seligmann, before resigning his position as Bacteriologist to the Inquiry, on leaving for Ceylon in December 1907, wrote an interim report of his work in which he gave his provisional conclusions. Conclusions arrived at by bacteriologists.

Dr. Cobbett and Dr. Graham Smith were then enlisted on behalf of the bacteriological work, and their results are to be found in detail in chapter xii. They came to a very definite conclusion as to the absence of pneumonia in the birds which they examined "in a perfectly fresh condition, the lungs being always pale pink in colour and free from congestion." They ascertained that the redness of the mucosa of the cæca was obviously not a *post-mortem* change. They concluded further that diseased birds as a rule have a very large number of *Trichostrongylus*, whereas healthy birds may have but few, and do not very often have a large number. They also came to the definite conclusion that "'Grouse Disease' is not an infection with those bacteria" which find their way in limited numbers into the organs of birds which contain *Trichostrongylus*.

They have not been able to satisfy themselves that the bacilli which find their way into the organs do much harm. Some harm no doubt they do; but how much they cannot say.

¹ A complete list of all birds examined, with a note of the principal lesions observed, is given in Appendix B.

Adam's view is that a potent cause of disease is the "constant absorption of small quantities of bacteria," hence the question put by Drs Cobbett and Graham Smith, "Is it a toxæmia caused by the poison liberated from bacteria which have been absorbed from the intestine, and which have almost immediately perished in the tissue?"

Their work has all tended to the view that Klein's observations required revision in the light of modern work in bacteriology, that his deductions required amendment, and that "Grouse Disease" is not an acute infectious pneumonia.

Can we then believe that there is an epidemic form of "Grouse Disease" which in spite of minute inquiry and search has eluded the vigilance of the Inquiry during the last six years?

Drs Cobbett and Graham Smith (*see* p. 274) go the length of saying: "It is, we suppose, just possible that we never came across the genuine epizootic 'Grouse Disease' at all."

Apart from the question of whether Klein's pneumonia has any existence in reality, all the outbreaks of disease amongst Grouse which have come under the observation of the Committee can be ascribed either to Strongylosis or to Coccidiosis, the only two diseases which the Committee now recognise as causing widespread mortality amongst Grouse.

It is quite clear that one of the most important signs of disease, whether it be Strongylosis or Coccidiosis, is a loss of weight. And this loss of condition, even to emaciation, which follows on Strongylosis, is a character to which full prominence is given by all writers about "Grouse Disease," though no measurement of actual weights had ever been recorded so far as was known before the present Inquiry began its work.

The omission to record weights in the past is the more to be regretted because the chief characteristic of the only other form of "Grouse Disease" which has been reported is the fact that the weight of birds that have succumbed to it remains normal.

Probably one of the most persistently quoted observations, which many sportsmen and gamekeepers still maintain to be a fact, is that in some epidemics there is a certain proportion of birds which succumb to so acute and virulent a form of "Grouse Disease" that they die before any loss of flesh or weight can have time to show itself, and before any change in the appearance of the feathers becomes manifest.

This view is founded not on actual measurement of weight, but on the bird's general appearance of good feather and normal weight, *as estimated by the observer* who takes the bird in his hand when it is found dead on the moor.

In most alleged outbreaks of "Grouse Disease" the birds have been collected and burned, or buried by the score in a soft moss-hag or under a rock. They were never weighed, and never carefully examined. Yet without careful weighing and examination it is impossible to come to any reasonable conclusion as to their condition or the cause of their death.

The Committee's field-observer has himself been present on several occasions when such birds have been picked up and passed from one to another of the keepers and the ghillies; full-feathered, richly-coloured hens, perhaps found almost warm but dead upon their nests. And these birds have been weighed in the hands and their weight guessed as fully normal, notwithstanding the condition of the breast, yet the spring balance has invariably proved appearances deceptive, except in the cases where accident has been the cause of death.

If the case is a hen whose feathers have been recently donned for nesting a most misleading impression of good condition is given even in a wasted bird, where the plumage has not been drenched with rain or bleached by sunshine. In the cocks it is different, for the feathers have not been changed for the nesting season, and the plumage is often worn and faded in comparison with the new, nesting plumage of the hen.¹

It is often hard to believe that a hen Grouse which has died in full nesting plumage, however thin and poor, is not actually heavier than the dingy cock bird of the same month. And if no rain has fallen on the hen since her death the comparison between her and the cocks which are found in all stages of disease, decayed, weathered and bleached, is even more misleading.

The point has now been too often tested to allow of doubt. No bird dies of Strongylosis without loss of weight. That some birds waste more and some less before succumbing to the disease is certainly true, the difference in this respect depends mainly upon the season; yet it must be conceded that sex and individual strength also make a difference.²

On one point the Committee can speak with entire confidence. During the whole period of the Inquiry, from 1904 to 1910, there has not been a single outbreak of "Grouse Disease" in which the birds died without loss of weight.

¹ *Vide* chap. iii.

² *Vide* chap. vi. p. 142.

While, therefore, it is possible that the virulent form of disease does, in fact, sometimes occur, it is also possible that the belief in it is entirely without justification, and is the result of inadequacy in method and inaccuracy in observation.

During the investigations of the Committee's observers, an interesting sidelight has been thrown on a possible connection between Coccidiosis and the earlier work of Tegetmeier on pneumo-enteritis.

In some Grouse-chicks dying of intestinal Coccidiosis, cysts were found in the bronchioles, bronchi, and trachea, but not in the lung-tissue itself, while the lungs of the young birds exhibited apparent symptoms of pneumonia. The coccidian cysts in the bronchioles might be capable of setting up sufficient irritation to account for the pneumonic symptoms. It is possible that there may be here some explanation of the pneumo-enteritis of earlier writers.

CHAPTER X

“GROUSE DISEASE”—*CONTINUED*—STRONGYLOSIS¹

PART I.—THE THREADWORMS (*Nematoda*)²

By Dr A. E. Shipley

PART II.—ON THE DEVELOPMENT AND BIONOMICS OF *TRICHOSTRONGYLUS*
PERGRACILIS

By Dr Robert T. Leiper

(I.) Family Strongylidæ

(i.) *TRICHOSTRONGYLUS PERGRACILIS* (Cobbold)

Synonym : *Strongylus gracilis* Cobbold

THIS round-worm was first described under the name of *Strongylus pergracilis* (Cobbold), by Cobbold,³ whose words we quote:—

“*Characters*.—Body filiform, finely striated, gradually diminishing History.
in front, uniform in thickness below; head bluntly pointed, with a simple oral aperture; tail of the male furnished with a bilobed bursa, each half supporting four pointed rays; spicules two, thick, and slightly divergent; tail of the female slightly swollen above the subterminal anal orifice, rather sharply pointed at the tip; vaginal opening situated at the upper part of the inferior sixth of the body.

“Length of male $\frac{1}{3}$ inch to $\frac{2}{3}$ inch; body $\frac{1}{400}$ inch in diameter, tapering anteriorly to $\frac{1}{2000}$ inch at the head; greatest breadth immediately above the bursa $\frac{1}{300}$ inch.

¹ The term “Strongylosis” is employed in this chapter to denote the disease caused by *Trichostrongylus pergracilis* (Cobbold); though it would perhaps be more strictly correct to name the disease *Trichostrongylosis*.

² Reprinted with slight alterations from the *Proceedings of the Zoological Society of London*, 1909.

³ Cobbold “Grouse Disease,” p. 16.

"Length of female mostly $\frac{3}{8}$ inch, sometimes very nearly $\frac{1}{2}$ inch; breadth above the tail $\frac{1}{10}$ inch to $\frac{1}{8}$ inch, narrowing at the extreme point to $\frac{1}{1000}$ inch; longitudinal diameter of the eggs $\frac{1}{10}$ inch, their breadth being $\frac{1}{10}$ inch."

Eight years later Cobbold described,¹ under the name of *S. douglassii*, a nematode which occurred in great numbers in the proventriculus of certain South African ostriches. Their presence was associated by the ostrich-farmers with a certain amount of disease, and with some deaths.

Finally, we have the species *S. quadriradiatus* recently described by E. C. Stevenson. It occurred in considerable numbers in the intestines of a flock of fancy pigeons which had been almost destroyed by a malady of unknown origin early in 1904. In his article upon this disease, Stevenson points out that the presence of a few nematodes in the cæcum of the pigeon causes little harm. If, however, the threadworms exist in large numbers, disease becomes manifest. This Stevenson attributes to two causes: the first is the loss of blood; but there is, I think, little or no evidence that these nematodes live on blood. The second cause is the piercing of the walls of the intestine,² which permits the bacteria in the contents of the alimentary canal to make their way into the peritoneal cavity, where they set up peritonitis. Evidence is gradually accumulating as to the occurrence of this, and some of the French authorities even think that such a perforation, made as a rule by *Trichocephalus trichiurus* (*dispar*), is one of the more common, if not the most common, causes of appendicitis in man. The presence of these worms further sets up an inflamed, catarrhal condition of the walls of the intestine, which leads to a debilitating diarrhoea and to general disorders of the digestive system. As in other cases, the nematodes doubtless give off toxins, the effect of which is largely confined to the nervous system and to the cells in the blood of the host.

The genus *Trichostrongylus* has recently been established by Looss³ to include certain forms which he has separated out from the large genus *Strongylus*. The

Structure. *Strongylus pergracilis* of Cobbold corresponds so closely in structure with the species described by Looss that I think there can be no doubt that it also should be included in the new genus. The suggestion made above

¹ *Journal of the Linnean Society*, London, "Zoology," xvi., p. 184, 1883.

² An actual perforation of the membrane is not in all cases necessary. There are examples of bacteria traversing the wall or parts of the wall of the alimentary canal which have been locally or temporarily weakened in some way.

³ "Centralblatt für Bakteriologie, Parasitenkunde," xxxix., p. 409, 1905.



FIG. 1. Male *Trichostrongylus pergracilis*, showing m mouth, alimentary canal, spicules, and genital bursa. Magnified.

FIG. 2. Female *T. pergracilis*, showing an. anus; c.gl. cephalic glands; m. mouth; oe. oesophagus; of. ovjector; o. ovary; ph. pharynx; r. rectum; ut. uterus with segmenting eggs; v. vagina. Magnified.

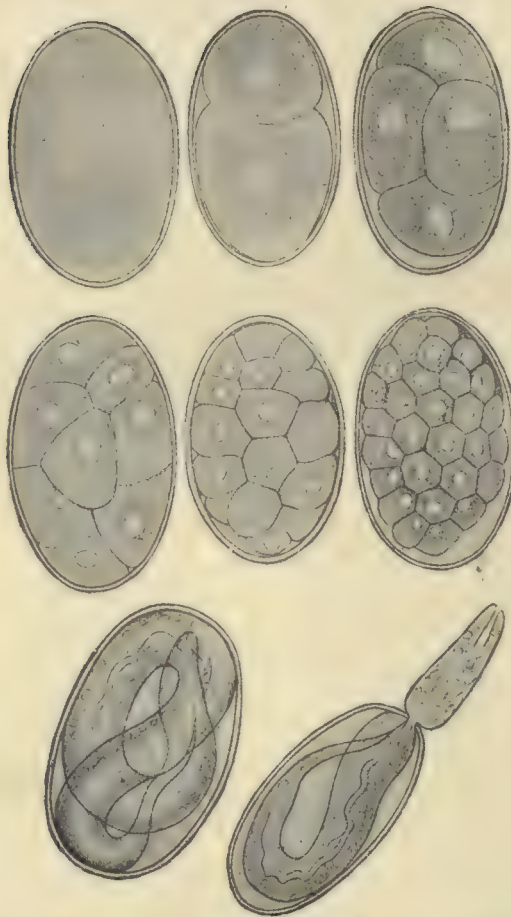


FIG. 3. Unsegmented egg. Egg with two blastomeres. Egg with four blastomeres. Egg with eight blastomeres, only six showing. Egg with blastomeres, all showing. Egg with sixteen blastomeres. Egg with thirty-two blastomeres. Egg with sixty-four blastomeres. Egg with coiled-up larva, ripe for hatching. A similar egg, artificially ruptured, and the larva in the act of escaping. This shows the contraction of the egg-shell when ruptured.

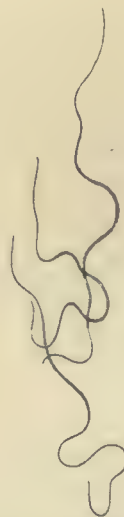


FIG. 4. Three specimens of female *Trichosoma longicolle*. Magnified about twice.



FIG. 5. A female *Trichosoma longicolle*. Magnified about seven times.

that *Strongylus tenuis* Eberth of the goose should also be reckoned as a species of *Trichostrongylus* was made to me by Dr R. T. Leiper.

Specimens of *T. pergracilis* are found in the cæca of most Grouse. They are apt to cover themselves with mucus and dirt, and are consequently hard to see and often overlooked. We have found them, with hardly an exception, in every one of the two thousand Grouse examined.¹ They are rendered opaque and white, and hence much more apparent, by shaking up the contents of the cæcum in 75 per cent. alcohol, to which a few drops of corrosive sublimate have been added. Their presence is also readily detected by compressing a drop or two of the cæcal contents between two microscope-slides and holding them up to the light. The worms, if there be any, then appear as thin, white, transparent lines. We owe this method to Dr Wilson.

T. pergracilis is an extremely fine worm, measuring in the male on the average 6 to 8 mm., and in the female 8 to 10 mm. They are very narrow and hair-like, and, as a rule, whitish in colour, but sometimes have the tinge of blood when seen in a very thin layer on a slide through the microscope. They are very transparent, readily revealing their internal structure, and they are so soft that the pressure of a cover-slip almost always ruptures them. The cuticle is very clearly and definitely ringed, and the rings are so constituted that whilst the worm can easily work its way forward through a tissue, it would have difficulty in wriggling backward. The rings give the edge of the body a strongly serrated appearance like a saw. This is most marked a little way behind the head, and extends over about one-third the body length. There is no trace of longitudinal marking on the cuticle (*vide* Pl. xxxiii., Figs. 1 and 2).

The genital bursa or expansion at the tail of the male is well formed, and opens by an oval opening with its long axis longitudinal. The bursa is supported by a number of ridges as an umbrella is by its ribs, and, using Looss's nomenclature, these are arranged in three groups. The members of each group arise from a common root and are recognisable, even when, as in the case of *T. pergracilis*, some of them run close to and parallel with members of another group. The three groups are: (1) Dorsal; (2) Lateral; (3) Ventral.

The spicules in the male are very conspicuous and very difficult to describe. They are short, strongly chitinised, with thickened edges and a kind of haft or base at the anterior end; and each spicule is hollowed something like a crumpled, withered, lanceolate leaf. Each spicule is provided with retractor and protractor muscles,

¹ *Vide* vol. ii, Appendix D.

and when protracted they are divaricated. When in this extruded condition they form a cross, the left spicule projecting to the right and *vice versa*. Besides the spicules and between them, rather to the posterior end, lies the accessory or median piece, which Looss calls the "gubernaculum." It is best seen in profile, and has then somewhat the outline of a Turkish slipper. It also has muscles inserted into its ends.

Near the base of each spicule is an oval clear vesicle; but apparently the end of the spicule was outside and not inside the lumen of the vesicle.

The head presents very little signs of differentiation. In some specimens with a one-twelfth objective three very minute lobes can be seen, but they are not visible in all cases, and their appearance may be due to some expansion of the mouth. The mouth is terminal and leads into a slightly bulb-like cavity which soon narrows into the thin capillary lumen of the alimentary canal. The oesophagus is more granular than the intestine, and separated from it by a very shallow groove; its walls consist of flatly rounded cells with conspicuous nuclei. I could not detect any parts in the intestine; it appears to be an undifferentiated tube running from mouth to anus, the lumen lined with chitin and the walls formed of granular cells with visible nuclei. No food was seen in the alimentary canal. Posteriorly the intestine widens into a spacious rectum, which just in front of the anus narrows again into a short, thin, terminal portion. The anus in the male opens into the genital bursa; in the female it is a little distance in front of the end of the pointed tail, but relatively not so far forward as it is in the larva. Two cervical glands run about a fifth of the length of the body backwards, and end with rounded ends about the same level.

In the male the testis begins about the level where these glands end. It consists of a single tube, the cells lining which give rise to the spermatozoa. Anteriorly the cells when squeezed out seem amoeboid, with rounded and very refringent nuclei. The hinder end of the testis is, however, crowded with spermatozoa shaped like little squat bottles, and in some specimens the genital bursa sheltered two clumps of these, looking as though they had escaped from the two vesiculæ seminales.

I saw nothing of excretory canals or their opening, and unless an ill-defined ring which surrounded the alimentary canal about one-twenty-fifth of the body-length from the anterior end be the nerve-ring, I saw nothing of the nervous system.

The ovaries are double. Each tube arises about the level or a little behind the

level of the hinder end of the cervical glands. One of them runs, with but slight undulations, straight to the "ovejector" which opens by the vagina, situated about one-sixth of the body-length from the hinder end, the other passes the vagina and reaches back almost to the anus; it then doubles forward again and opens into the posterior "ovejector."

The anterior end of each ovary contains undifferentiated protoplasm, but soon eggs begin to appear. At first these are very flattened, like a pile of coins, much broader than they are long; then they become thicker, and, finally, three or four times longer than they are broad. The rounded nucleus is in every stage very conspicuous. It is impossible to say precisely where the ovary ceases and the oviduct begins. We find the long cylindrical cells rounding themselves off, and an egg shell beginning to appear. By this time fertilisation must have taken place, but I have not seen any spermatozoa in the oviduct. The oval cells usually lie at first with their long axis at right angles to the longitudinal axis of the oviduct; then, when a little older, they lie obliquely, and, finally, they come to lie with their long axis parallel to that of the duct, in which position they are most readily swallowed by the "ovejector." The anterior and the posterior oviducts usually contain one, two, or three unsegmented ova; then come some six to eight segmented eggs representing as a rule the stages with two, four, eight, sixteen, thirty-two, sixty-four, and sometimes a hundred and twenty-eight blastomeres. One or two of these stages may be represented by two ova, but in any case the segmentation must be very rapid (*vide* Pl. xxiii., Fig. 3).

The lower end of the oviduct is lined by what, in optical section, appear to be high columnar cells with very granular disintegrating borders. These seem to be secreting something. The walls of the oviduct pass suddenly into the "ovejector," which consists of three parts: (a) The most internal is somewhat funnel or trumpet-shaped, its wider mouth is continuous with the walls of the oviduct and is crenellated; the funnel is richly supplied with both longitudinal and circular fibres; not infrequently it contains an egg. (b) The second chamber of the "ovejector" is spherical, very transparent, and is marked by the presence of a large number of radiating muscle-fibres running from the periphery to the limits of the lumen. The contraction of these fibres would enlarge the lumen and suck the egg on. (c) The third chamber of the "ovejector" is thin-walled, with a chitinous lining. It frequently shelters an egg. At its outer end it narrows, and uniting with the similar narrow end of its fellow it forms an extremely short vagina which opens to the exterior by a longitudinal slit, the edges of which are also crenellated (*vide* Pl. xxxiii. Fig. 2).

The ova are laid in the fluid contents of the host's cæca in which they are frequently found floating. We have found developing ova in the cæca of a young Grouse chick of seven to ten days of age from Auchentorlie, Dumbartonshire. Apparently the cæca are the chief centres of absorption of the digested food; they contain none of the cellulose skeletons of vegetable cells so common in the intestine, and none of the masses of cast epithelium which make up so large a proportion of the flocculent masses in the duodenum. The eggs *may* develop further inside the cæcum, though as yet we have not found an egg containing an embryo in its contents.

A small pellet of the cæcal contents, such as can be carried away on the point of a needle spread out under a cover-slip, will, in a well infected bird, show some twelve to twenty worms and one hundred to two hundred eggs in the field of a two-thirds inch Ross's objective with a No. 2 eyepiece.

Allied species. In his Memoir on the genus *Trichostrongylus*, Looss enumerates the following four species:—

(1) *T. RETORTÆFORMIS* (Zeder), 1800. From the duodenum and exceptionally from the stomach of *Lepus timidus* and *Lepus cuniculus* (when undomesticated). Railliet says it coexists with *Strongylus strigosus*, and helps to give rise to a pernicious anæmia. It develops directly without intermediate host.

(2) *T. INSTABILIS* (Railliet), 1893. Syn. *T. subtilis* Looss, 1905. From the duodenum and exceptionally from the stomach of *Ovis aries*, *Ovis laticauda*, *Antilope dorcas*, *Camelus dromedarius* (Egypt), *Papio* (*Cynocephalus*) *hamedryas* (North Africa), and occasionally in Man (Egypt and Japan). Railliet states that this species, together with *Hæmonchus contortus*, lives in the duodenum of sheep which succumb to pernicious anæmia.

(3) *T. PROBOLURUS* (Railliet), 1896. From the duodenum of *Ovis aries*, *Ovis laticauda*, *Antilope dorcas*, and occasionally of Man (Egypt), and *Camelus dromedarius* (? Paris and Egypt).

(4) *T. VIBRINUS* Looss, 1905. From the duodenum of *Ovis aries*, *Ovis laticauda*, occasionally from *Camelus dromedarius* and Man (Egypt). Looss regards this as a rare species.

To these must be probably added:—

(5) *T. TENUIS* (Eberth), 1861. Syn. *S. tenuis* (Mehlis) Eberth, 1861. From the cæcum of the goose, *Anser cinerea*, and

(6) *T. NODULARIS* (Rud.), 1809. Syn. *S. nodularis* (Rud.), 1809. Syn. *Ascaris mucronata* Fröhlich, 1791; *S. anseris* Zeder, 1800; *S. nodulosus* Rud., 1803; *S. crispinus* Molin, 1850. From the mucous and muscular coats of the stomach and

duodenum of various species of the family Anatidæ. They are said to be very fatal to young geese.

(7) *T. PERGRACILIS* (Cobbold), 1873. Syn. *S. pergracilis* Cobbold, 1873. From the cæcum of *Lagopus scoticus*.

(8) *T. QUADRIRADIATUS* (Stevenson), 1904. Syn. *S. quadriradiatus* Stevenson. From the intestines of pigeons.

(9) *T. EXTENUATUS* (Railliet), 1898. Syn. *S. gracilis* M'Fadyean, 1897, not Leuckart, 1842. This form occurs in the fourth stomach of cattle in England, and in cattle, sheep, and goats in the United States.¹

(10) *T. CAPRICOLA* Ransom, 1907. From goats and sheep in the United States.

It is noticeable that this genus of parasite occurs only in vegetable feeders, and that, whereas it lives always in the stomach or the duodenum of mammals, it chiefly inhabits the cæca of birds.

PARASITES OF *TRICHOSTRONGYLUS PERGRACILIS* (Cobbold).

In a female specimen two amœboid organisms were making their way along the body-cavity in the region of the "ovejector." Each was throwing out rounded pseudopodia, and the distinction between the granular endosarc and the glassy ectosarc was very sharp. Another specimen had some refringent bodies, in shape like short rows of yeast-cells or fungi-spores, lying in the body-cavity.

The life-history of *Trichostrongylus pergracilis* (Cobbold) is described by Dr Leiper in Part II. of this chapter.

(ii.) *SYNGAMUS TRACHEALIS* (Von Sieb).

The Red or Forked-Worm.

We have found this common pest of the fowl-yard and pheasant-coop but twice in the Grouse. Probably the free and unconfined life of the Grouse, together with the comparative paucity of earthworms on the moors, protects Grouse from the "gapes," as the disease caused by the forked-worm is called. Earthworms abound in Scotland in the cultivated lands, pastures, and woodlands, and occur even on the tops of mountains. Mr Wm. Evans tells me he has a list of seventeen species of the Lumbricidæ taken north of the Tweed, but they are practically absent from the peat-moors, where heather, Grouse, and humic

¹ B. H. Ransom, U.S. Department of Agriculture, Bureau Animal Industry, Circular 116, 1907.

acid are most abundant. Some moors, however, such as those on the Pentlands, include patches of land in which worms flourish. Still there seems no reason at present to incriminate the forked worm of causing any trouble to Grouse. One of our cases was a young bird from Argyllshire.

(II.) Family *Trichotrachelidæ*.

(iii.) *TRICHOSOMA LONGICOLLE* (Rud.).

Synonyms: *Calodium caudinflatum* Molin.

Trichosoma gallinum Kow.

Trichosoma caudinflatum Kow.

HISTORY.

This genus, first named and described by Rudolphi,¹ is also described by Dujardin² from various species of gallinaceous birds. He gives a list of the earlier and ill-defined synonyms. The species is also mentioned by Diesing³ under the same name. It is recorded by Molin⁴ under the name *Calodium caudinflatum*, the name referring to the swollen tail of the female, from the small intestine of the partridge and the quail. Eberth,⁵ who gives the best account of the anatomy of the genus *Trichosoma*, gives a short description and a figure of a nematode under the same name, *Trichosoma longicolle*; he draws attention to Dujardin's description of a funnel-like appendix to the vagina, and surmises that this is a prolapsed piece of the vagina; this is undoubtedly the case in some of our specimens. Kowalevsky⁶ mentions under the name *Trichosoma gallinum* what Dr von Linstow tells me is this species, and in a later paper⁷ apparently describes and figures this under the name *Trichosoma caudinflatum*. Unfortunately I have been unable to read this, as the paper is written in Polish. Railliet⁸ considers that the *Trichosoma longicolle* described by Dujardin and Eberth does not agree with Rudolphi's description of his *Trichosoma longicolle*. He points out that Dujardin and Eberth's species occurs in the cæcum of the fowl and of the guinea-fowl, and he renames this species *Trichosoma retusum* Raill., 1893. The length of this worm

¹ C. A. Rudolphi, "Entozoorum Synopsis." Berlin, 1819.

² M. F. Dujardin, "Histoire Naturelle des Helminthes," p. 19.

³ C. M. Diesing, "Systema Helminthum," ii. p. 260, 1850-51.

⁴ R. Molin, "Sitzungsberichte der kaiserlichen Akademie der Wissenschaften," xxxiii. p. 302. Wien, 1859; and "Denkschriften der kaiserlichen Akademie der Wissenschaften," xix. p. 330. Wien, 1861; also Mem. 1st Veneto, ix. p. 617, 1860.

⁵ C. J. Eberth, "Untersuchungen über Nematoden." Leipzig, 1863.

⁶ M. Kowalevsky, "Bulletin international de l'Académie des Sciences de Cracovie," p. 280, 1894.

⁷ M. Kowalevsky, "Rozprawy i Sprawozdania z posiedzeń wydziału matematyczno-przyrodniczego Akademii Umiejętności," xxxviii. p. 274. Kraków, 1901.

⁸ A. Railliet, "Traité de Zoologie Médicale et Agricole." Paris, 1895.

is 13 mm. in the male, 19 mm. in the female. Rudolphi's worms—which may belong to more than one species—vary from 39 to 80 mm., and have been described from *Lyrurus (Tetrao) tetrix*, the Black Grouse, Black-cock, or Grey-hen; *Tetrao urogallus*, the Capercailzie; *Gallus gallinaceus*, the Common Fowl; *Phasianus colchicus*, the Common Pheasant; *Chrysolophus (Phasianus) pictus*, the Golden Pheasant; *Perdix cinerea*, the Common Partridge; and *Coturnix communis*, the Common Quail.

We first found specimens of *T. longicolle* in a Perthshire Grouse which was brought us in the morning we were leaving Blair Atholl for the south in the autumn of 1906. Having once seen it, however, it was soon observed again, though it occurs sparingly. It always lives in the duodenum, sometimes associated with the tapeworm *Hymenolepis microps*, and sometimes alone. The worms resemble short pieces of very fine white silk (*vide* Pl. xxxiii., Figs. 4 and 5).

This species has two longitudinal rows of dark spots irregularly scattered in two lateral bands. Roughly speaking, there are five or six of the spots in a transverse row; but they are not regularly arranged. The two bands arise anteriorly in the region of the œsophagus, and as they pass backward they become somewhat narrower, much more pronounced in appearance, and darker. Each spot corresponds with a unicellular gland, and the bands of these glands replace the ordinary nematode excretory system in the Trichotrachelidæ, the family to which *Trichosoma* belongs. They have been best described by Jägerskiöld.¹ Each cell opens by a minute straight duct which traverses the cuticle and forms what used to be called the rod-shaped body. The *Trichosoma longicolle* of Eberth² has a third or ventral band, and he mentions that Dujardin saw but one band in his specimens.

The length of the specimens varied from 20 mm. in the male to 40 mm. in the female. The greatest breadth of the body was $4.5\ \mu$, but in the neck-region it did not exceed $3\ \mu$, and tapered away to the anterior end, where the breadth was but $0.5\ \mu$. The very regular large cells in the region of the neck, which are pierced by the œsophagus, are just under $3\ \mu$ in width and are $12\ \mu$ in length. In the young specimens these cylindrical cells with flat ends, lying like a lot of pillars end to end, are not cut up into a series of segments, which gives a scalloped outline to the cells of the adult when seen in profile. But later a number of circular constrictions arise, and these divide each cell into a series of ten or twelve areas

¹ "Kongliga Svenska Vetenskaps-Akademiens Handlingar," xxxv. ii., 1901.

² "Untersuchungen über Nematoden." Leipzig, 1863.

upon each side, and the whole cell has the appearance of being built up of two rows of rounded bricks lying side by side in a double pile. The nucleus remains large, oval, and conspicuous. At the end of each cell there is usually a dark granulation which serves very clearly to define their limits.

The lumen of the œsophagus which pierces these peculiar cells is very minute, and is lined with a definite chitinous tube. The "cellular body," as the aggregate of the œsophageal cells is sometimes called, ends abruptly, about one-fifth the body-length from the anterior end. Here the œsophagus passes quite abruptly into the capacious intestine with its many-celled walls. Just at this point, and tucked away in the angle formed by the minute œsophagus widening into the broad intestine, are a couple of glands, probably the homologues of the cervical glands of other nematodes. The intestine continues to the hinder end of the body with no change; it is somewhat difficult to distinguish, as it is just about the same brown colour as the lateral lines. The posterior end of the female is truncated, and the anus is at the ventral side of the abruptly terminated body.

The ovary is a single tube which anteriorly contains undifferentiated eggs. These gradually attain a definite and somewhat irregular outline. Posteriorly the ovary opens into a spacious uterus, in which the ova are oval, with a distinct vitelline membrane. The uterus is broad, and serves, with its contents, to conceal the other organs of the body. Posteriorly, where the body is wide, the ova are irregularly crowded together; there may be as many as five or six ova in a transverse row. Further, towards the head the ova acquire their characteristic egg-shell with two bright spots at each end. They closely resemble the eggs of *Trichocephalus trichiurus* (*dispar*). About halfway along the body the diameter lessens as we pass forward, and after a certain space the uterus is narrowed and only permits a couple of eggs to be abreast, and finally the eggs are reduced to a single row. The uterus opens by a vagina which is situated a little way behind the end of the "cellular body," *i.e.*, just behind the anterior end of the intestine. The uterus or vagina is usually prolapsed and forms a bell-like structure, one edge of which usually has a clear oval vesicle in its walls. Through this bell-shaped structure the eggs pass out.

The male is markedly smaller than the female. Its average length is about 25 mm. and its width throughout does not surpass the anterior end of the female's body.

The testis is a single tube which opens posteriorly. At the tail end the male has a pair of cuticular folds or flanges, possibly representing a genital bursa. There is a single spicule, very long, and in many cases only perhaps protruded for a

fourth or fifth of its whole length. It is described as having a sheath; but in the specimens we have seen this was not apparent—probably it was retracted.

The males are very much rarer than the females—in fact, we examined a considerable number of specimens without finding a single male: probably they occur in about the proportion of one to seven or ten females. We have occasionally found a very long, thin larva in the duodenum, which we take to be the larva of the Trichosome.

The eggs appear to undergo no segmentation in the body of the worm, and, in fact, we have not yet seen an egg of *Trichosoma longicolle* segmenting. In one Grouse from Ross-shire small embryos of some nematode were found in the small intestine. It is possible that these are the young of *T. longicolle*, but they show no trace of division into neck and body. It is also possible that they are the larvæ of *Trichostrongylus pergracilis*; but they differ in size and shape from those young of this species which we have hatched out and found free. The Grouse in which they were found have been feeding on corn, and I am rather inclined to believe that these larvæ are the young forms of *Tylenchus tritici* which causes the well-known "corn-cockle."

Trichosoma longicolle occurs only in the duodenum, often associated with the species of *Hymenolepis* which inhabits this part of the alimentary canal. They are surrounded by epithelial cells, singly and in clumps, and of many sizes and shapes, which have been shed in immense numbers from the wall of the duodenum. These may have been detached by *post-mortem* digestion. These worms have been found in 13·6 per cent. of the birds examined; but it must not be forgotten that they are most inconspicuous and easily overlooked. They have been found in Grouse from Montgomeryshire and Yorkshire, as far north as Ross-shire, and at all seasons. They do not occur in large numbers, and their pathological effect seems small; still we must not forget that their near ally, the human parasite *Trichocephalus trichiurus* (*dispar*), is one cause of peritonitis and appendicitis in man.

However the nematode makes its way into the chick, it must, like the *Trichostrongylus*, grow very rapidly. We have found specimens in a Grouse-chick of fourteen days in age.

(III.) Family Ascaridæ.

(iv.) *HETERAKIS PAPILLOSA* (Bloch).

Stossich¹ mentions this round-worm, under the synonym of *H. vesicularis* Fröhl, as occurring in the Grouse. It is a very common parasite in poultry and

¹"Glasnikhrvatskoga naravoslovnoga druztva," *Societas historico-naturalis Croatica*, p. 284, Zagreb, 1887.

pheasants. It occurred in the hand-reared birds at Frimley, and Dr Cobbett and Dr Graham-Smith have found twenty-three in one cæcum and ten in the other in a Grouse from Abbeystead which was free from *T. pergracilis*, and one in each cæcum of a Grouse from Longtown, Cumberland, which had one hundred and eight *T. pergracilis* in one cæcum and one hundred and twenty-seven in the other, and the same number similarly distributed in a bird from Bolton Abbey, which had three thousand one hundred and eighteen *T. pergracilis* in one cæcum and two thousand eight hundred and seventy-seven in the other.

(IV.) Family Filariidæ.

(v.) *FILARIA SMITHI* (Sambon.)

Dr Sambon¹ has described a microfilaria or larval form of some species of *Filaria* in the blood of Grouse. The adult forms of such larvæ usually live in the lymphatics and subcutaneous tissues; their larvæ pass into the blood, and are conveyed to new hosts by some blood-sucking insects.

PART II.—ON THE DEVELOPMENT AND BIONOMICS OF *TRICHOSTRONGYLUS PERGRACILIS*

By Dr Robert T. Leiper

In view of conclusive evidence accumulated by the Inquiry regarding the constant presence of a small threadworm *Trichostrongylus pergracilis* in the cæca of nearly all sick adult Grouse, it became a matter of importance to study in some detail the life-history of this parasite with a view to determining the manner in which it is reproduced and disseminated, the mode of infection of healthy birds and, if possible, to obtain experimentally the symptoms of "Grouse Disease" under artificial conditions. In order also to have some reasonable basis of fact upon which to establish preventive and curative measures, a knowledge of the conditions favourable to and inimical to the growth of the parasite at its various stages of development became necessary. The present section deals with the results of an inquiry into these problems.

The parasites are exceedingly fine hair-like worms of about one-third of an inch in length, and of a pale pink colour, but of such transparency as to be almost

¹ See "Journal Tropical Medicine and Hygiene," x, p. 304, 1907. *Filaria smithi* cannot, however, stand as the name is preoccupied by Cobbold's species, *Filaria smithii*, from the elephant. *Transactions of the Linnean Society of London*, 2nd.

invisible to the naked eye. They live in the cæcal portions only of the intestine of the Grouse. The sexually mature females give rise to their progeny as eggs, which undergo a certain degree of development while still within the body of the worm. By the time they are laid the egg content has become subdivided into a large number of cells,

Develop-
ment
within
body of the
Grouse.

forming what is technically known as the *morula* (Fig. 16). As *morulæ* these

eggs pass into and mix with the contents of the cæca, all further development thereupon ceasing. This suspension of development appears to depend upon a lack of some necessary stimulant in the cæcal contents, for the eggs may be found alive and at the same stage not only several days, but even so long as a month after the death of the bird. In nature the cæca are evacuated periodically, and the ova thus pass out of the body with the soft portion of the bird's dropping. In one or two cases where a portion of the cæcal contents had passed into the rectum, and had there become diluted somewhat by the fluid from the

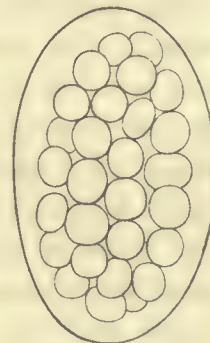


FIG. 16.
Morulæ of eggs.

great intestine, eggs were found to have progressed to the formation of an embryo while within the body of a dead bird; but such a condition is obviously abnormal, and does not invalidate the general conclusion that the eggs of this parasite require to pass out of the body of the bird before they are able to continue their growth, and that, in consequence, the parasites within the body cannot increase in number by sexual multiplication. Each and every parasite found within the body of the Grouse must therefore have actually entered it from the outside. We shall see later that this explains the apparent anomaly that whereas practically all Grouse are infected with *Trichostrongylus* only some suffer from the disease. The egg, when newly passed, measures 0·075 mm. by 0·046 mm. and contains a morula composed of about sixty-four cells.

If a freshly passed cæcal dropping be isolated and kept uncontaminated no further development will take place in the ova contained in it. A fungus will gradually grow upon it, and owing to this and bacterial con-
tamination the eggs eventually die. If the dropping be exposed to the drying influence of sun and wind, as on the moors during summer, it becomes caked and dry, and the eggs die. If, on the other hand, cæcal dropping be spread out in such a way as to admit of the whole becoming

Develop-
ment of the
egg outside
the body.

oxygenated by the atmosphere, and it be also slightly moistened, development will proceed, its rapidity increasing with the temperature.

Cultural
methods. For the experimental study of the extra-corporeal development the following method was found most reliable.

Petri dishes, as used in-bacteriological research, of a diameter of about 4 inches, were employed in pairs. Into the upper dish was placed a closely fitting piece of thick blotting paper, which was thoroughly moistened with water. The inside of the lower dish was smeared uniformly with a very thin layer of cæcal dropping or cæcal content taken direct from a dead bird. Several drops of water were then added and mixed into the viscid layer by means of a glass microscopical slide so as to produce a glairy mixture that would but slowly slide off the Petri dish when it was held almost upright. The layer of fæces should be sufficiently thin to allow of an examination under the microscope with a two-thirds inch lens. The upper Petri dish was then placed over the lower dish, forming a close chamber, the atmosphere of which quickly became saturated with water vapour. From time to time the Petri dish was opened and a small quantity of fæces removed on a platinum wire for microscopical examination, or the lower part was placed upon the stage of the microscope and directly observed.

A similar method, and one which permitted the study of the various stages of development in a small number of eggs, was the use of hanging drop dishes.

If the former of these two methods has been adopted, in the course of twelve hours the colour of the culture in the Petri dishes should have changed from a greenish yellow to a reddish brown, and a sickly sweetish odour, similar to that found in lactic acid fermentation, should have become distinctly appreciable. Otherwise experience teaches that putrefactive processes will almost certainly set in and lead to the destruction of the eggs and worms in the culture. After the eggs have hatched, and when minute worms are seen wriggling through the culture, it will be found advantageous to leave the Petri dish open for several hours in order to allow of the evaporation of some of the water, and the culture to acquire more consistency.

A larger amount of water appears to be necessary for the growth of the young parasite previous to hatching than afterwards. Indeed we shall see later that a certain amount of consistence appears to be absolutely necessary for the full growth of the young worm.

In the culture made by the above method the egg mass continues rapidly

to segment until the resulting cells are exceedingly small. The mass becomes somewhat flattened, and a slight dimple appears at one border of the oval disc (Fig. 17). This is the first step towards the formation of the cylindrical body of the young embryo. By the gradual deepening of this dimple the egg mass acquires a tadpole-like appearance, the anterior end being, thus early, easily distinguished from the posterior end of the body. The anterior portion soon exhibits a central depression, which indicates the commencing formation of the mouth (Fig. 18). As the lateral dimple continues to deepen the body mass elongates to such an extent as to become folded upon this two or three times, in order to become accommodated within the shell (Fig. 19). The alimentary canal meanwhile has gradually been developing, so that by the time the embryo attains a cylindrical form the canal is found to extend throughout the body as a distinct cell-walled tube (Figs. 20, 21). During the whole of this period the embryo remains quiescent, but about an hour or so before it leaves the egg-shell it commences to exhibit a certain amount of movement. This movement gradually increases

Develop-
mental
changes in
ovum.

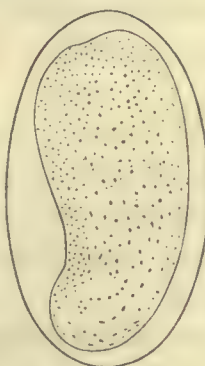


FIG. 17.

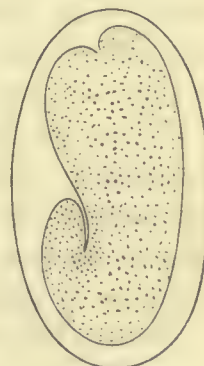


FIG. 18.

Developing ova of *T. pergracilis*.

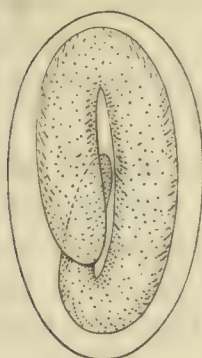


FIG. 19.



FIG. 20.



FIG. 21.

Formation of the larva of *T. pergracilis*.

in extent and vigour, until it ultimately overtakes the resistance of the egg shell, which suddenly ruptures. The success or failure of these efforts on the

part of the young worm appears to depend on the amount of water which is imbibed from the outside, for if only such an amount of water be added to the culture as is absolutely necessary to set the process of development in motion, and the culture be then allowed to dry somewhat, it will be found that the embryo is incapable of rupturing the egg shell. A slight collapse of the egg shell, owing to an insufficiency of water, causes the death of the embryo at any period of its growth. Hatching usually takes place in from thirty-six to forty-eight hours after the egg passes out of the bird; but in summer it may be delayed for even as long as a month.

When the embryo is hatched there seems little purpose in its early movements. The cuticle, at first irregularly crinkled, gradually smoothenes as the parasite becomes saturated with water. The movements now appear to gain in purpose, and very soon the little worm is actively moving about, obviously in search of food.

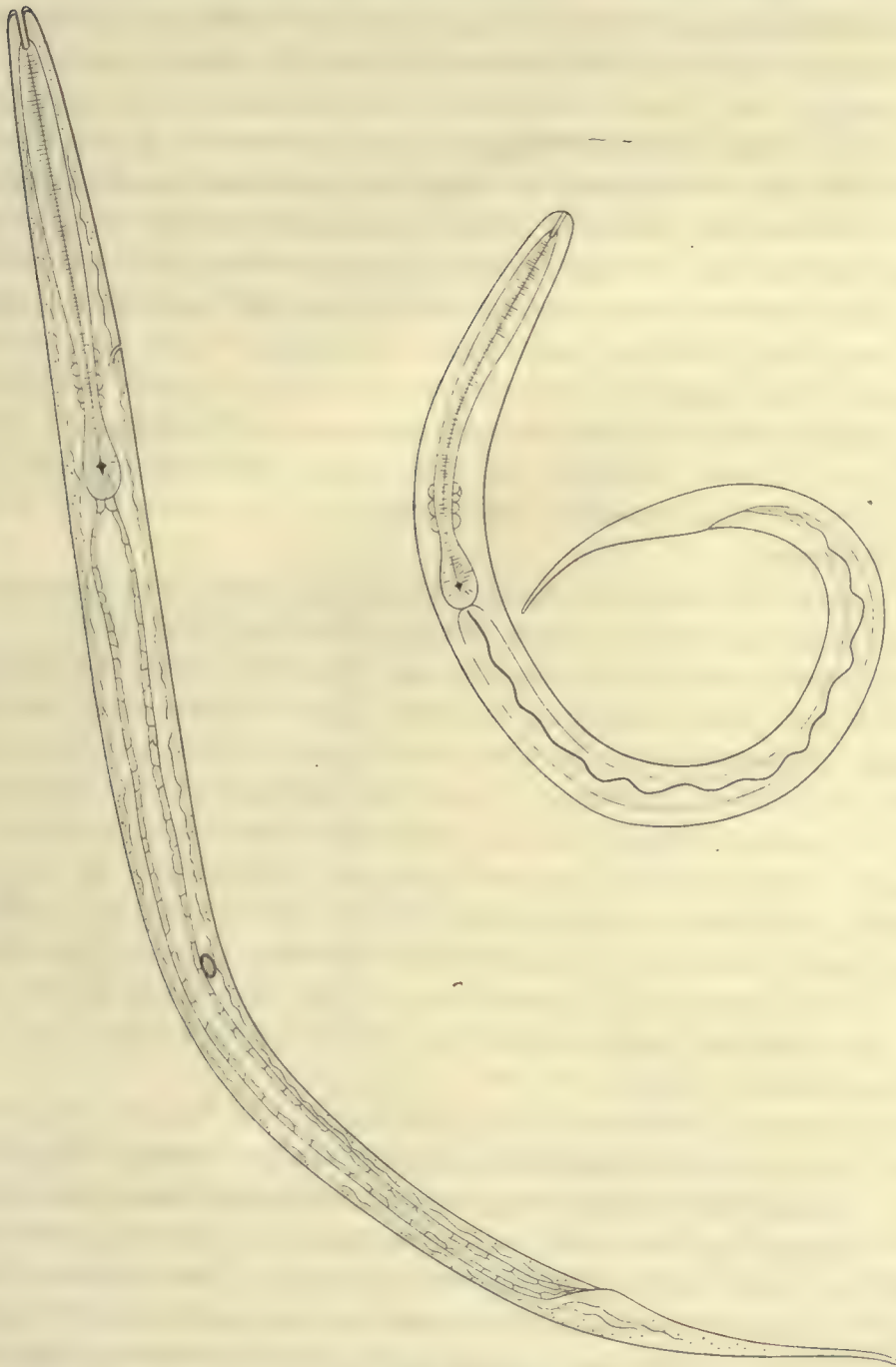
When newly hatched, the embryo measures 0.36 mm. in length, and 0.015 mm. in greatest thickness (Fig. 22). The cuticle shows no regular striation. The body is cylindrical, tapering to a slender pointed tail in the last 0.1 of a mm. of its length. Anteriorly it maintains an almost uniform diameter to within 0.05 of the mouth, when it shows a slight and gradual narrowing. The anterior extremity ends bluntly, and has a diameter of 0.0075 mm., presenting at its summit the small rounded opening of the mouth capsule. At 0.06 mm. from the tail the anal pore opens with but little external indication.

Anatomical characters of the embryo.

Alimentary Canal.—Two faint parallel lines are seen running inwards for a distance of 0.01 mm. from the oral pore. These are the walls of a cylindrical mouth capsule, which later, with the growth of the worm, become much more thickened and obvious.

The œsophagus measures 0.1 mm. in total length, and is divided into two portions. The anterior two-thirds is cigar-shaped, uniting by a narrow neck with the posterior one-sixth which becomes bulbous. Surrounding this narrow neck are a number of large refractile cells, forming the nerve ring of the central nervous system. The œsophageal portion of the gut discharges into a long chyle intestine. The epithelial cells of its wall lie at first almost in touch, and the lumen is visible merely as a long, fine, wavy streak passing along the centre of the body. The rectum is short, 0.01 mm. in length, and is cuticular.

Upon the success of the embryo in obtaining a plentiful supply of food depends almost wholly its future growth. If a freshly hatched embryo be



FIGS. 22 AND 23.
Newly hatched embryos of *T. pergracilis*, highly magnified.

transferred to plain water it will live for several days, but show no growth or further development. Evidently there is only a sufficiency of reserve substance within the ovum to develop the embryo to the time of hatching. When there is enough food, but the medium is very aqueous, the worm requires to exert itself to a much greater extent in order to entrap small solid particles of food into its rigid and chitinous mouth capsule. If, however, the culture is of such consistency that the embryo is able, by burrowing its way through the faecal matter, to force this into its mouth capsule, there follows a very rapid growth in size and early differentiation of tissue, even when there is a marked lack of oxygen. Under these favourable conditions of food supply an embryo increases in size to such an extent that on the fourth or fifth day from the commencement of the culture it is obliged to shed its cuticular covering. At this time thousands of very delicate sheaths may be found floating in the culture for a few hours; but they very rapidly disappear.

The embryo now measures about 0.46 mm. in length, the oesophagus 0.12 mm., the anus line 0.08 mm. from the tip of the tail (Fig. 23).

An *excretory pore* is to be seen 0.09 mm. from the anterior end of the body, and at 0.24 mm. from the anterior end there is now visible a small clear globule 0.005 mm. in diameter lying on the ventral surface between the body wall and the wall of the chyle intestine. This is the rudiment of the future genital system. A marked difference is now noticeable in the chyle intestine. Three large well-developed valves are seen governing the entrance to it from the oesophagus. Its lumen is widely dilated, 0.01 mm. in diameter, and is filled with ingested faeces. The cells of the gut wall are flattened and very finely granular.

No gross structural alterations accompany this first moult or ecdysis, but during the succeeding three or four days certain changes within the body of the worm gradually become evident.

The cylindrical mouth capsule (Fig. 24) slowly loses its clear cut border and appears to be undergoing absorption, and its lumen decreases (Fig. 25). At the same time the oesophagus lengthens, the bulbous posterior portion becomes pyriform, and later merges into the anterior portion, but so gradually as to be only definable with difficulty. The cuticular lining of the whole oesophagus, and the marked triradiate lining of the oesophageal bulb (Fig. 24) become resolved into a simple thin cuticular covering (Figs. 25, 26). The walls of the intestine, which have gradually increased in size, become more

The first
moult or
ecdysis.

The meta-
morphosis.

clearly defined, and now appear as cylindrical turgid cells distended with large globules of highly refractile substance, giving the larva a characteristic appearance by which it can be readily distinguished from free-living nematodes (Fig. 26).

The whole body appears to have slightly narrowed during the process of metamorphosis, by the conclusion of which the larva has become changed into a slender actively moving worm, with a simple elongated oesophagus without mouth capsule (Figs. 26, 28). Accompanying the metamorphosis in structure is a marked change in habits, for instead of burrowing into the denser portions of the food

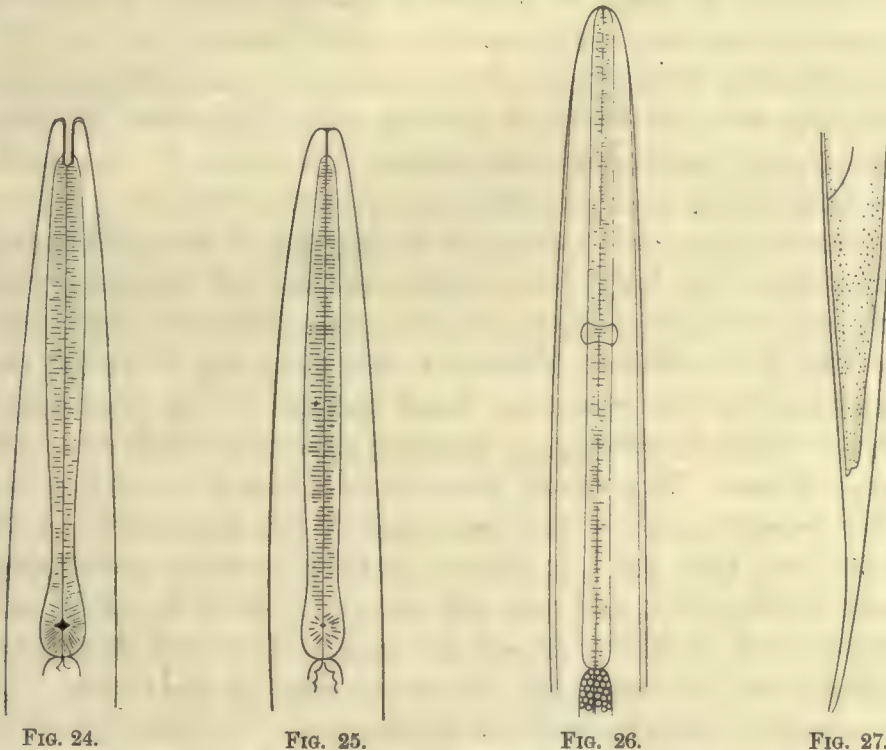


FIG. 24.

FIG. 25.

FIG. 26.

FIG. 27.

Changes in *T. pergracilis* during ecdysis and encystment.

these metamorphosed forms now rush about with great rapidity, and either wriggle into the patches of open water or make their way on to the actual surface of the culture, and may be seen standing out in numbers into the moist atmosphere above, forming a kind of hoar frost on the surface of the fæces apparently in search of oxygen. Those larvæ, which are fortunate enough to be near the edge of the culture, ascend in the condensed water on the sides of the Petri dish and make their way on to the upper part, eventually reaching the blotting paper.

Others will crawl out of the thin edge of the culture medium and become stranded on the dry glass. This metamorphosis takes place between the eighth and sixteenth day from the commencement of the culture, the difference in time depending almost entirely on the temperature at which the culture is kept.

If the blotting paper be now removed, and the upper part of the Petri dish be put aside, so that the moisture on its inner surface, which contains the actively wriggling metamorphosed larvæ, be allowed to evaporate slowly, it will be noticed that as the water disappears the movements of the larvæ gradually diminish and eventually entirely cease, so that ultimately the larvæ lie sometimes making irregular figures like notes of interrogation, sometimes coiled up like a watch spring (Fig. 29). If drying proceeds sufficiently slowly it would be found on examining the dish with a hand lens, that when all traces of moisture have disappeared the little coiled larvæ stand out as turgid, glistening streaks. They seem to be capable in this condition of retaining a certain amount of moisture within their thick resistant cuticle for several days, and to make up for any loss of fluid by evaporation by slowly retracting the body from either end and of detaching themselves from their cuticular skin (Figs. 26, 27, 30). This retraction may go on to such an extent that if one suddenly adds water once more to a Petri dish containing such dried forms the little worms are found enclosed in long sheaths that extend much beyond each end, recalling the sheathed embryos of filaria seen occasionally in the blood of man. This second formation of a sheath, or as it is sometimes called, the "encystment," is the last stage of the development of the larvæ outside the body (Fig. 30). It appears to be a necessary preliminary to the attainment of infectivity, and once this stage is reached the larvæ can remain alive without food or further growth for weeks. The larva does not shed this second sheath until it reaches the alimentary canal of the Grouse. There are thus two moults in the extra-corporeal development. The first is completed prior to metamorphosis; the second, subsequent thereto, is not completed during the non-parasitic period.

So much then for artificial experiments.

The following details of an experiment made during August 1909 serve to illustrate what actually becomes of the hatched worms under natural conditions upon the moors. A culture made in the manner described above was taken to a small village, on the coast of the Bay of Cardigan, where no Grouse lived or had been known to exist for many years.

The second
moult or
"encyst-
ment."

Larval
migrations
on heather.

Some young plants of bell heather were sought, and eventually two or three small suitable plants were detached uninjured from crevices in rocks. These were planted in a Petri dish, and the dish was half filled with water so as to cover the roots. The plants were then set aside. A week later they were found to have survived the transplantation, and to have commenced to grow

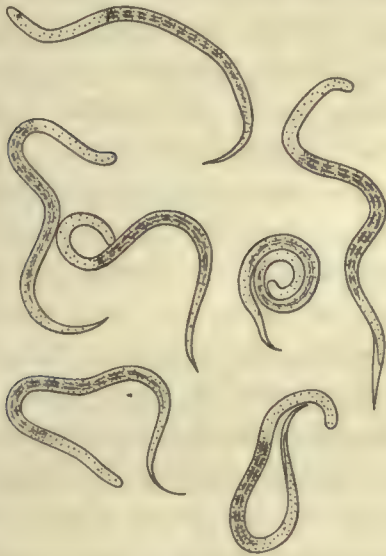


FIG. 28.

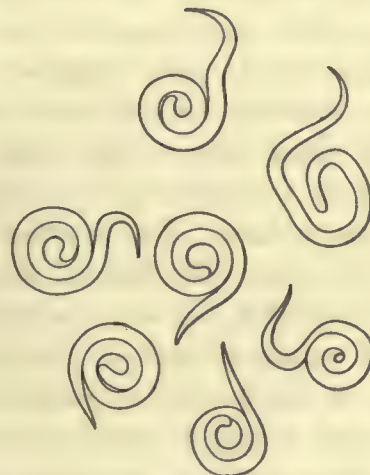


FIG. 29.

Larvæ forms of *T. pergracilis*



FIG. 30.

Encysted larvæ of *T. pergracilis*.

under the new conditions. As the weather was showery the plants and dishes were left out in the open, and for two or three days in succession the raindrops hanging from the tips of the heather were microscopically examined. They were found to be almost free of life. On one occasion, however, a small free living nematode was found. Although slightly resembling the larvæ of *Trichostrongylus pergracilis* it was readily distinguished from them by its microscopical characters.

Immediately after one of these periodical examinations, the culture of *Trichostrongylus pergracilis*, in which the majority of the larvæ had just undergone metamorphosis, was poured into the water round the roots of one of the experimental plants. The plant was left out in a typical "Scotch mist" for a couple of hours. At the end of that time raindrops were again taken from the highest tips of the heather, which were about $3\frac{1}{2}$ inches above the surface of the water, and they were found to be literally swarming with the actively wriggling metamorphosed larvæ of *Trichostrongylus pergracilis*. These larvæ had ascended the wet stems and leaves of heather against the current of water that was trickling down towards the roots. Their intense activity was doubtless due to the large amount of oxygen present in the fresh rain. The plant was then taken from the Petri dish and placed in a cardboard box, which was sealed down. A month later the box was opened. The heather was found to be alive still and growing, but very dry. The tips of the shoots from which the raindrops had been taken were cut off and soaked in little watch glasses of fresh water, and in the course of half an hour there wriggled out from the crevices of the leaves of the heather a considerable number of larvæ, showing at either end the long collapsed parts of the sheath which as we have already seen are characteristic of the larvæ that have undergone drying under artificial conditions. The intestine showed the characteristic refractile appearance already noted.

The following synopsis of the life-history of this parasite may be of interest as summarising the order and minimal duration of the various stages of life-history in the life-cycle.

- April 1. Egg in morula stage passes out of Grouse.
 „ 3. Larva hatches out and lives in dropping or in moist earth.
 „ 5. First moult or ecdysis.
 „ 8. Metamorphosis, larva now in actively migrating form.
 „ 9 (or after). Larva ascends to tips of heather; if there is no mist, rain, or dew the ascent will be postponed.
 „ 10 (or after). Encystment or drying; this represents the first stage of the second moult—an indefinite interval may intervene here.
 „ 10. Larva swallowed by Grouse, and completes second moult.
 „ 11. Reaches cæca of Grouse.

April 13. Completes his hypothetical third and fourth moults, thereafter become adult and sexually productive.

„ 13. Pairs as soon as adult stage is reached.

„ 14. Lays eggs in cæca.

„ 15. Eggs pass out of Grouse.

Thus the exact mode by which the worms attain to the most favourable conditions for infecting the Grouse had been determined, for the young growing tips of heather are those most sought after by the birds. It remained to be seen whether the administration of these metamorphosed encysted larvæ to healthy Grouse would result in the actual production of *Trichostrongylosis*.

It is related elsewhere in the Report that the administration of eggs and embryos of the *Trichostrongylus pergracilis* and of centrifugalised washings of heather from the moors to healthy uninfected Grouse had given uniformly negative results. From the observations described above the explanation of these failures becomes very evident. The eggs and embryos of the parasite require to undergo certain essential developmental changes for a period of almost a fortnight's duration before they acquire the power of infection when swallowed by Grouse. The forms got from the heather were undoubtedly non-parasitic nematodes and their young, for these bear a general resemblance to the unmetamorphosed embryos of *Trichostrongylus pergracilis*—many of them having a very similar type of mouth capsule. Moreover, the embryos of *Trichostrongylus pergracilis* do not acquire their migratory habit until they have become metamorphosed, and therefore do not ascend the heather until they have entirely lost their oral capsule.

Experi-
mental
induction
of *Tricho-
strongylosis*.

Until the above described experiments were successfully concluded the characters of the metamorphosed larvæ were quite unknown, and therefore it was impossible that they should have been recognised in washings of heather.

Owing to the fact that the deliberate administration of Grouse fæces to healthy Grouse for the purpose of scientific observation is considered to be a form of vivisection (accidental infection occurs continually on the moors), and owing to the desirability that the various experiments of this character should be carried out by one member only of the Committee, the cultures were handed over to Dr Wilson for the purpose of administration to hand-reared Grouse at the Frimley experimental station.

On June 19th, 1909, the culture which had just undergone metamorphosis, and which was therefore in the active migrating stage, was administered to an adult male bird one year old. The droppings of this bird were entirely free from *Trichostrongylus* ova when the experiment was begun. An examination of the fæces on the successive days showed that no infection had taken place. By June 26th the culture had undergone further development changes, and showed a large number of encysted forms. A dose was again administered by Dr Wilson, and some four days later ova of *Trichostrongylus pergracilis* were found in the droppings. The number of ova increased on successive days. On July 3rd a further dose of the same culture, now thirty days old, was administered. The bird died five days later, showing distinct loss in weight, the presence of a large quantity of chalky fluid in the rectum, and the cæcal contents red with blood. From the *post-mortem* examination I came to the conclusion that the bird had been killed by the passage of some of the last culture into the lungs, for there was considerable pneumonia, and quantities of the culture were found in the fine tubules.

This first experiment was therefore not wholly conclusive as regards the actual induction of *Trichostrongylosis* by the administration of encysted metamorphosed *Trichostrongylus pergracilis* larvæ. It served to establish, however, that these larvæ can reach the cæca of the Grouse, attain their adult condition, and become sexually productive in the very short space of four days. It also demonstrated that the sudden invasion of the cæca by a large number of *Trichostrongylus pergracilis* produced such a marked effect upon the mucous membrane as to fill the cæca with blood.

In the second experiment made by Dr Wilson my culture was much older, and contained encysted forms. The doses were repeated periodically, with the result that in the course of two and a half months the bird fell in weight from 17 ounces to $11\frac{3}{4}$ ounces. The cæcal droppings were as full of *Trichostrongylus pergracilis* ova as those of a bird suffering from *Trichostrongylosis*, and the bird itself showed a similar condition of progressive weakness and emaciation. The mucous membrane of the cæca was covered with *Trichostrongylus pergracilis*, but no evidence of extravasation of blood into the lumen of the cæca was found on the death of the bird. Apparently that seen in the first case must have been associated in some way with the development of the parasite before reaching maturity.

These two experiments indicated in so far as such a limited number may,

that this parasite in very large numbers has a marked pathogenic action upon Grouse, inducing loss of weight, progressive wasting, and in extreme cases, death. An examination of serial sections of the cæca in heavily infected Grouse shows that here and there the mucous membrane is penetrated by the anterior end of the worm; but no evidence was obtained from the sections that such penetration led to the local invasion of the tissues by intestinal bacteria. The presence of *eosinophilia* in the blood as demonstrated by Dr Fantham indicates that certain substances secreted or excreted by the parasite pass into the circulation.¹ These, together with the loss of function of the cæca, owing to the extensive decortication of the epithelial lining by the worms, seem to me to sufficiently account for the resulting symptoms of the disease. The final invasion of the general circulation by bacteria represents the terminal phase in the progress of the disease, and not an essential factor in its causation. Most adult Grouse suffer also from a slight degree of Coccidiosis. This parasite to a much greater extent destroys the epithelial lining, so that were the common disease amongst Grouse primarily the result of invasion by intestinal bacteria, the coccidia should play a more important rôle than the *Trichostrongylus* in the causation of the symptoms of "Grouse Disease." Yet it is well known that the droppings of adult birds may show evidence of considerable infection with coccidia without any symptoms of disease being apparent. Death of adults from Coccidiosis apparently only results from an intensity of infection not met with on the moors, but only in the hand-reared birds or birds experimentally infected.

Significance of
eosinophilia.

If it be accepted that *Trichostrongylus pergracilis* is the primary and essential factor in the production of the common form of "Grouse Disease" remedial measures must be directed either to the destruction of the adult parasite within the bodies of the birds, or of the young forms during their stay outside the body.

Remedial
measures.

The impracticability of the former of these two methods is obvious. The birds are unapproachable, and are spread over a very wide area. Vermifuges or antihelminthics are expensive and more or less poisonous substances, the dosage of which has to be carefully estimated and controlled. The problem therefore resolves itself into that of destroying the eggs and larvæ of the parasites during their stay outside the body.

The destruction of the eggs or embryos by surface dressing with cheap

¹ *Vide* chap. xiii. p. 316.

chemical substances would appear at first sight to be a hopeful line of action, but the occurrence of the cæcal droppings more or less all over the moor, and the enormous area requiring treatment, render any such methods futile. Moreover, as we have shown, the larvæ after a brief period of development ascend the heather and can remain hidden in the crevices of the leaves, in a quiescent, invisible and living state for a prolonged period. The only conditions that could be inimical to these, the infective forms, would be atmospheric conditions

Effect of frost. of marked severity, possibly a prolonged frost or a prolonged drought, or destruction of the infected heather by fire or cutting. The effect of extreme cold has been tested by subjecting the metamorphosed larvæ to freezing in the cold storage rooms at the Albert Dock for a period of a week. On being thawed out of the solid block of ice it has been found that they quickly regained their activity. Exposure to slow drying, on the other hand, under experimental conditions, results in the death of the encysted larvæ.

Effects of drought. Death from lack of moisture must be continually taking place on the moors, although there may often be, even at the hottest parts of the day, an insensible transpiration from the growing plant, sufficient to maintain the life of the larvæ by preventing desiccation. Burning and cutting appear to be the only practical means by which infected heather plants can be properly purged.

To one more or less unaccustomed to the moors it is a matter of astonishment to notice what might be described as the extraordinarily insanitary condition of the Grouse's home. Nearly every square yard of moorland shows traces of fæcal deposits, and forcibly directs attention to the fact that there is an unnatural over-population of the moors.

When one remembers that practically all Grouse are infected with *Trichostrongylus pergracilis*, and that from every dropping thousands of potential parasites normally emerge, it becomes evident that the greater the number of birds upon a given area, the greater in turn must be the infecting capacity of the moor. But on most moors only a very small proportion of the heather is suitable for food for Grouse at certain times of the year,¹ and as the Grouse is a very heavy feeder it follows that the parts of the moor from which the food supply is derived are just those likely to be the most heavily contaminated with droppings.

The number of birds on a moor should be correlated, not with the size of the moor but with the extent of the suitable food area thereon. The amount

¹ *Vide* chap. iv. p. 71.

of stock on a large moor may seem very low proportionately to the whole area, but when estimated in proportion to the food area it may prove exceptionally high, and this means a high potential capacity for the production of *Trichostrongylosis*, whilst the entrance of a few bacteria or protozoan parasites into the body may suffice to cause serious diseases owing to the rapid multiplication of the original germs. In helminthic infections, as we have shown, the parasite *cannot* multiply inside the bird. Birds with few worms remain healthy. The progress of the disease is correlated with the actual number of parasites entering and surviving in the body. The more heavily infected the food, the more heavily infected does the bird become.

The following facts connected with the growth of the parasite outside the body of the Grouse emerged from our Inquiry, viz.: (1) that moisture is necessary for the development of the egg; (2) that a minimal temperature of several degrees above freezing point is essential not only for the development of the egg, but also for the metamorphosis of the embryo; (3) that the embryo ascends the heather only after metamorphosis. These facts afford us some explanation of the disease being a fatal one in the spring months. During the summer months many of the cæcal droppings must be dried by the sun and wind shortly after they are passed, and the eggs thereby killed. The same agencies must also desiccate beyond revival a large number of the encysted larvæ upon the heather. During the winter months, however, this loss does not occur. Owing to the low temperature and continual wet the eggs remain in a living but quiescent condition. Even if an occasional spell of warmer weather occurs, and the eggs develop into embryos, it would be necessary that such period of high temperature should continue for at least a fortnight to enable these embryos to become converted into active migrating larvæ. The result probably is that there accumulates upon the moors during the whole winter vast numbers of undeveloped eggs and unmetamorphosed embryos. The low temperature does not kill them, but merely suspends their growth for the time being. At the spring-time the minimal temperature rises gradually to such a point as to allow the continuous development of the eggs and embryos to and through metamorphosis, with the result that at this period there presumably ascends the heather the accumulated result of fæcal contamination during the winter months. The frequent rains and mists give the larvæ ample opportunity to reach the topmost tips of the heather at this time.

Practical
facts
established.

The rapid death of the eggs of *Trichostrongylus pergracilis* in fæces that have undergone temporary drying indicates that the drier the moor, the more efficacious will wind and sun prove as natural antagonists to "Grouse Disease." Again, as the infective forms of the parasite occur on the "food" heather, it is evident that the greater the amount of "food" heather in proportion to each bird, the less likely it is to become infected.

As the periodical burning of heather increases eventually, not only the area of food heather, but at the same time destroys in the only effective way known the living parasites upon the area of heather burned, the policy of heather burning, advocated by other members of the Committee upon other grounds, receives additional support.

The practicability and value of a periodical cutting of the heather requires further consideration by those acquainted with local conditions; but, if practicable, such a measure should not only be a means of ridding large areas of the moor of infective material, and of bringing about a rapid increase in the "food" heather area, but might also be applicable to those parts of a moor and in those seasons of the year when burning is impossible.

CHAPTER XI

"GROUSE DISEASE"—CONTINUED—COCCIDIOSIS

By Dr H. B. Fantham

PART I.—THE MORPHOLOGY AND LIFE HISTORY OF *EIMERIA* (*COCCIDIUM*) *AVIUM* A SPOROZOÖN CAUSING A FATAL DISEASE AMONG YOUNG GROUSE¹

I. INTRODUCTION.

The subject of this memoir is a microscopic, protozoal parasite, which infests the lining epithelium of the alimentary canal of Grouse. It belongs to the Coccidia, a group of parasitic protozoa, many of which are known to occur in the digestive tracts of both vertebrates and invertebrates. These minute organisms reproduce by means of resistant spores, and belong to that class of the protozoa known as the Sporozoa. The Coccidia are of economic importance, inasmuch as they destroy the mucous membrane of the intestine of the host, thereby setting up enteritis which is accompanied by diarrhœa, and very often has a fatal effect upon the unfortunate animal harbouring the parasites, especially if the host be young.

Such a disease—termed Coccidiosis—has long been known in rabbits, and is often fatal. Occasionally Coccidiosis occurs in man. The life-history of a coccidian parasite is complicated. There are two phases in the life-cycle:— (1) a multiplicative phase within the cells of the gut-epithelium of the host, and (2) a reproductive phase leading, after a sexual act, to the formation of resistant spores adapted for life outside the body of the host. The spores so formed are the means of spreading the parasite, and lead to the infection of fresh hosts. The two phases were formerly considered to belong to separate parasites; but the occurrence of alternation of generations in the life-cycle of Coccidia was first suggested by R. Pfeiffer in 1892, conjugation was discovered in Coccidia by Schaudinn and Siedlecki (1897), and the complete life-cycle was demonstrated with a wealth of morphological and cytological

¹ Reprinted from the *Proceedings of the Zoological Society of London*, 1910.

detail in the celebrated memoir of the late Dr Schaudinn (1900) on *Eimeria* (*Coccidium*) *schubergi*, parasitic in the gut of the centipede *Lithobius forficatus*.

Coccidia have been recorded from most of the great groups of the metazoa, but very few coccidian life-histories have been investigated completely.

Dr Leiper, while working on helminthiasis in Grouse in May 1909, noticed the occurrence of coccidian cysts in large numbers in the gut of many Grouse chicks, with concomitant enteritis, very often proving fatal. The coccidian cysts are oval, and at first sight might easily be mistaken for eggs of worms. Dr Leiper suggested that Coccidiosis was a factor in "Grouse Disease," especially in young birds. Early in June 1909 I spent some time on one of Lord Lovat's moors in Scotland for the purpose of investigating Coccidiosis in Grouse chicks.¹ Previously we had noticed, at various times, the occurrence of Coccidian cysts in adult Grouse, but not in large numbers. I have much pleasure in expressing my thanks to Lord Lovat, Dr A. E. Shipley, Dr E. A. Wilson, Dr Hammond Smith, and Dr Leiper for aiding my researches by procuring material for me, and to Professor Nuttall, in whose laboratory much of my work was done. I also availed myself of the services of the Secretary of the Committee, who placed me in communication with a large body of correspondents through whom I obtained further material to enable me to continue the investigation, and to whom my thanks are tendered.

In this paper I wish to record my researches on the morphology and life-history of *Eimeria avium*, more especially as it occurs in the Grouse. I would point out that the length of time at my disposal for these researches has been limited, only *one* season being available to me for procuring material, and I have had several other investigations to consider during the period, so that I was not able to give undivided attention to the elucidation of the protozoa of Grouse. However, the complete life-cycle of *Eimeria avium*, responsible for the dwindling of Grouse broods in spring, is here set forth for the first time, so far as I am aware.

II. THE GENERIC NAMES *EIMERIA* AND *COCCIDIUM*.

Unfortunately, owing to the rule of priority, the generic name *Coccidium* (Leuckart, 1879) no longer holds, but is replaced by that of *Eimeria* (A. Schneider, 1875). I am in sympathy with Professor Minchin, when he writes in a recent review:—"We regret to see the familiar generic name *Coccidium* replaced by *Eimeria*; this is one of those many cases where, in our opinion, rebellion against

¹ The number of Grouse chicks dying of Coccidiosis on the moors is not easily estimated, for the chicks die in the heather, and their tiny corpses are rarely found.

the law of priority in nomenclature is not only lawful but imperative" (*Nature*, March 3rd, 1910). It would save much confusion if the question of zoological nomenclature were settled by an international committee,¹ as has been suggested by many able workers.

The Coccidia of birds were first recorded in Fowls by Silvestrini and Rivolta (1873), under the name *Psorospermium avium*. Subsequently Railliet and Lucet (1891) recorded Coccidia from fowls, naming the parasite *Coccidium tenellum*. I have followed Doflein (1909) in naming the Coccidia of birds *Eimeria avium*. The coccidian parasites were obtained from Grouse chicks, and I have succeeded in transmitting the Coccidia of Grouse to fowl chicks and to young pigeons.

III. METHODS.

In this investigation of Coccidiosis both fresh and preserved materials were used. Samples of gut contents, taken from different regions, were examined fresh, and often these have been fixed wet with osmic or formalin vapour, and stained by Delafield's hæmatoxylin or by Giemsa's stain. Such smears were sometimes useful for examining merozoites.

Oöcysts, because of the chitinous and almost impenetrable character of their walls, had to be examined fresh.

For preserved material, the best fixatives were found to be Schaudinn's fluid (corrosive-acetic-alcohol) and Bouin's fluid (picro-formol-acetic), to which a few drops of absolute alcohol were added. Schaudinn's fluid tends to shrink the tissues, while Bouin's fluid requires much washing out. Sections, 5μ to 6μ thick, were made of the duodenum and cæcum of infected birds, these parts of the digestive tract being especially examined. The chief stains used were Delafield's hæmatoxylin (either alone or counterstained with orange G or eosin), which was found to be most useful, safranin and lichtgrün, iron-hæmatoxylin (with or without Van Gieson's picro-fuchsin), and paracarmine. On the whole the hæmatoxylin proved of most service.

On diluting some of the cæcal contents or fæces of a Grouse chick suffering from Coccidiosis, and examining the preparation microscopically, numerous oval cysts are seen (Pl. XXXVII., Figs. 61-66). Sometimes the cysts are also seen in the small intestine just beyond the duodenum. These cysts may have homogeneous contents, or, when older, may show four more or less well

¹ The subject of zoological nomenclature is now (1911) being so considered.

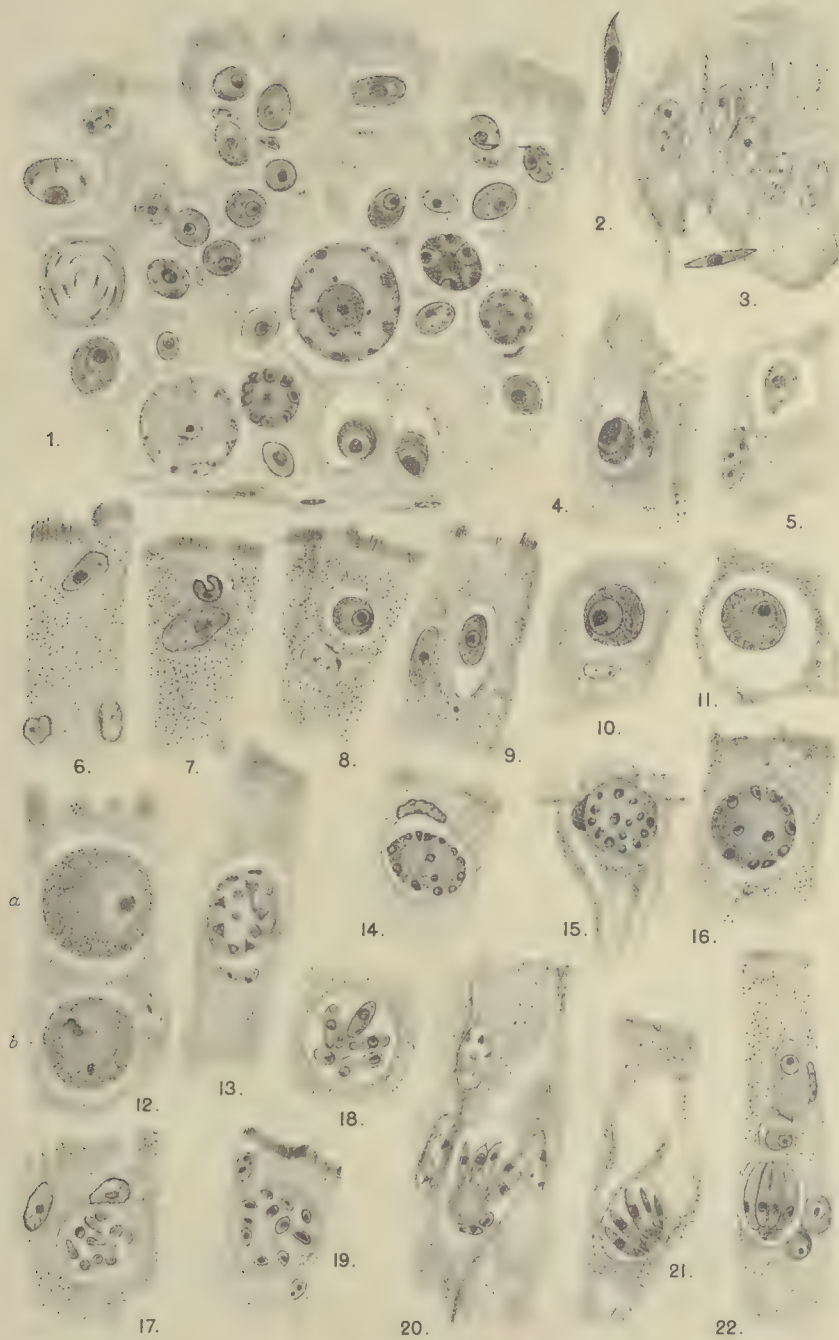
differentiated sporocysts within them (Figs. 67-70). Each sporocyst, if ingested by another Grouse, can develop two active, motile germs or sporozoites (Figs. 71-76), which can penetrate the intestinal epithelium—especially of the duodenum—and so begin a new infection. Though the oöcysts and spores are the most obvious external manifestation of Coccidiosis, it is usual, and certainly more convenient, to begin the life-cycle of the *Coccidium* with the minute sporozoite (Pl. xxxiv., Fig. 2), the agent whereby primary infection is brought about.

The sporozoites are minute, falciform, or vermicular bodies (Pl. xxxiv., Fig. 2) capable of fairly rapid movement, and possessing great penetrative powers. They measure from 7μ to 10μ in length. The ends of the sporozoite are rather pointed, the extremity that moves foremost being slightly more acuminate than the posterior end. The general body cytoplasm is more or less homogeneous, exhibiting but very fine granulations. The nucleus has a definite rounded or oval contour. The chromatin is evenly distributed throughout the nucleus.

When the sporozoites are liberated from the investing sporocyst (Pl. xxxvii., Figs. 74-76), by the action of the pancreatic juice of the Grouse, they are capable of active movement. The usual method of progression resembles that of the sporozoite or motile trophozoite of a gregarine. The organism moves forward with a slow gliding movement, the forward progression being facilitated by the secretion of a viscid proteid substance that rapidly hardens. On the smooth surface thus provided the coccidian sporozoite glides forward. The track of the sporozoite, as shown by its trail, can be stained, and the organism then shows the gelatinous or proteid material issuing from near the posterior region of its body (Pl. xxxiv., Fig. 2). During the gliding movement waves travel down the body of the sporozoite, recalling what is seen on a larger scale in the billowy undulations of the foot of a snail. On other occasions a more rapid movement of the sporozoite occurs. The two ends of the organism become approximated and then rapidly straightened, the effect being to propel the organism forwards much more quickly than when the gliding movement alone is used.

The sporozoite thus makes its way to an epithelial cell of the duodenum and proceeds to penetrate the cell. As it forces its way inwards (Pl. xxxiv., Figs. 3, 4), so the sporozoite curves on itself (Fig. 7) and becomes round and immobile (Figs. 5, 6, 8). The young, rounded parasite (Figs. 8-10) is now on the trophic phase of existence, and continues to grow for some time, feeding passively on the food-materials of the host-cell. During this period the parasite is called a trophozoite (Figs. 8-12a).

PLATE XXXIV.



H B Fantham del

E Wilson, Cambridge.

EIMERIA (COCCIDIUM) AVIUM.
(Schizogony)

The nucleus of the trophozoite is approximately central in position, or sometimes to one side, and at first contains scattered granules of chromatin. It then becomes somewhat vesicular (Figs. 8-11), and gradually the chromatin collects into a central karyosome, lying within the nuclear sap (Fig. 12a). The position of the karyosome, however, is not always centrally fixed; it may lie to one side of the nucleus (Figs. 8, 10).

The growth of the trophozoite naturally affects that of the host-cell. The protoplasm of the latter becomes more and more tenuous, great hypertrophy of the host-cell occurring. This condition is maintained for some time, and finally a limit is reached and atrophy sets in, the nucleus of the host-cell then appearing as a small, often crescentic mass (Figs. 10, 14) to one side of the film (Fig. 12) that represents the host-cell. A clear space often intervenes between the parasite and the enveloping epithelial film (Figs. 9, 11, 12).

The trophozoite, having attained its full size (some 10μ to 12μ in diameter) within the host-cell, proceeds to divide, and the result of its division is to increase the number of parasites within the host. This stage in the existence of *Eimeria avium* is known as the schizont (agamont), and the method of multiplication is termed schizogony.

The schizont (Fig. 12) is a more or less spherical parasite. At first it is uninucleate (Fig. 12a), but soon its nucleus begins to fragment (Fig. 12b). The division of the nucleus of the schizont is of the nature of multiple fragmentation rather than of a series of binary fissions of the nucleus and karyosome (Figs. 13-18). The parasite is very small, and it is not easy to follow the cytological details, even under the best and highest powers of magnification. Some of the portions of chromatin in multiple fragmentation may sometimes appear connected by thin strands (Fig. 13) for a short period, but the fragments soon travel to the periphery of the schizont. The small daughter masses of chromatin, at first homogeneous, gradually show differentiation, becoming minutely vesicular with a dot of chromatin usually to one side (Figs. 14-16), but occasionally central. Thus the nuclei of the future merozoites are forming their karyosomes early.

The daughter nuclei having migrated to the periphery of the mother cell (Fig. 16), the cytoplasm of the schizont concentrates around them, forming small ovoid masses (Figs. 18, 19). The daughter-forms so produced are the merozoites (agametes) which measure 6μ to 10μ in length. They gradually acquire a vermiform shape, and arrange themselves around the remains of the protoplasm of the mother

cell like the segments of an orange or the staves of a barrel (Pl. xxxiv., Figs. 20-22; Pl. xxxv., Figs. 23, 24). Owing to this method of grouping, the merozoites are said to be arranged "en barillet." The groups, when ripe, soon break up, and the individual merozoites are liberated. The movements of the merozoites, when free, resemble those of the sporozoites.

The number of merozoites formed from a single schizont seems to vary. Eight to fourteen seem to be common numbers, but as many as twenty have been found.

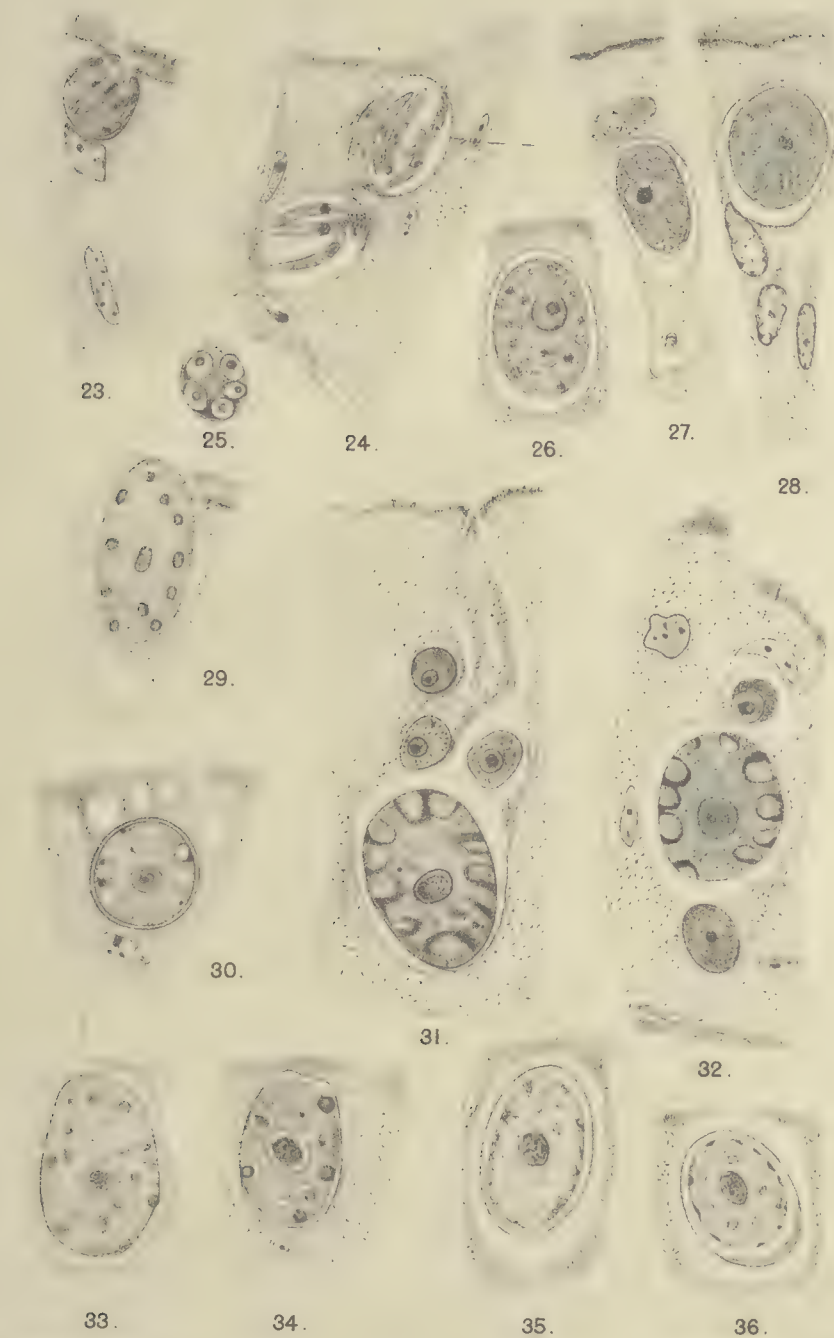
The merozoites finally are slightly curved vermicules (Pl. xxxv., Figs. 23, 24), possessing a nucleus which may be approximately central (Pl. xxxiv., Figs. 20, 21) or somewhat towards one end (Pl. xxxiv., Fig. 22; Pl. xxxv., Fig. 23). The nucleus of the merozoite is small, and the presence of a karyosome is often not very evident, though there is a small granule of chromatin—representing the karyosome—usually to one side of the nucleus (Fig. 24). The ends of the merozoites are rather less pointed than those of the sporozoites, a feature that *E. avium* has in common with *E. schubergi* as described by Schaudinn.

When the merozoites reach a new host-cell, they enter, become round, and proceed to grow as trophozoites in the same way as did their parent organism, and undergo later nuclear fragmentation in a similar manner. As the result of this, many more merozoites are produced, and as schizogony may be continued through several generations, the destruction of the gut-epithelium is very extensive (Pl. xxxiv., Fig. 1).

Towards the end of schizogony—especially in the cæcum—relatively smaller schizonts with larger and fewer merozoites (Fig. 25), about five in number on the average, are produced. These larger merozoites appear to be formed near the end of infection, in company with large numbers of gametocytes, so far as evidence is available.

These differences in the schizonts might be taken by some investigators to be indicative of difference in species—in other words, that more than one species of *Coccidium* may occur in the gut of Grouse. I do not state that this is not so, but personally prefer the view that the differences in the schizonts and merozoites noted are reflexes of the condition of nutriment of the parasite. Wenyon (1907) has some interesting observations on the variations in the schizogony of *E. falciformis* in the mouse, and states that the variations are due to the nourishment available for the parasite. Again, the species found in the liver and gut of the rabbit (*Coccidium oviforme* and *C. perforans*) are now usually united into one species, *Eimeria stiedæ*.

PLATE XXXV.



H B Pantnan, del

E Wilson, Cambridge

EIMERIA (COCCIDIUM) AVIUM.
(Macrogamete formation.)

The merozoites originally produced in the duodenum pass lower down the gut and reach the cæca. At the ileo-cæcal junction the epithelium is attacked again, and the merozoites rapidly grow to schizonts, which produce new generations of merozoites, so that the cæca soon contain very large numbers of the parasites.

Probably Coccidiosis set up in the duodenal wall is sufficient to kill very young chicks, *e.g.*, chicks eight to ten days old, while older chicks dying at the age of about four to six weeks may have partially recovered from duodenal Coccidiosis, but succumb to Coccidiosis in the cæcum (typhlitic Coccidiosis). In cases of intense duodenal Coccidiosis, merozoites are found free in the intestinal contents, and even in freshly shed fæces.

Sooner or later a limit is reached, both to the power of the Grouse chick to provide nourishment for the parasite, and to the multiplicative capacity of the parasite itself. In other words, the host begins to react on the parasite. Consequent on the now unfavourable environment, the parasite proceeds to form gametes, in order that its species may be perpetuated. The gametocytes or mother cells of the gametes (Pl. xxxv., Figs. 26-28; Pl. xxxvi., Fig. 37) are modified schizonts which are of slow growth, and therefore can accumulate more reserve food material in the form of granules within their cytoplasm. The processes leading to the formation of the gametes may be termed gametogony, which we may now consider.

Sexual differentiation is characteristic of the gametes of Coccidia, and in the case of *Eimeria avium* the differentiation is apparent in the gametocyte phase. Two forms of gametocytes can be distinguished. The first group are intra-cellular parasites containing large granules of food reserve within their cytoplasm. These are the macro-gametocytes (Pl. xxxv., Fig. 26) which give rise each to one female gamete. On the other hand, the micro-gametocytes (Pl. xxxvi., Fig. 37) or male progenitors contain a little reserve food material in the form of very minute granules, distributed evenly throughout the body substance. Each micro-gametocyte gives rise to many microgametes.

The structure of the macro-gametocyte and of the single macrogamete that arises from it is very difficult to interpret in *Eimeria avium*, on account of the large amount of reserve food material contained within the cytoplasm. Further, it is very difficult to draw the exact dividing line between the macro-gametocyte and the female gamete, as the one gradually merges into the other. These forms vary from 11.8μ to 17.5μ in length by 6μ to 11μ in

breadth, as seen in sections. Many relatively large granules occur in the cytoplasm of the macro-gametocyte. As the macro-gametocyte grows from round to ovoid, these granules gradually concentrate to form larger, roundish, hæmatoxylin-staining granules, which are albuminoid (Pl. xxxv., Fig. 29), the chromatoid granules of many authors. There are also other, non-basic staining, granules known as plastinoid granules ("granules plastiques" of Thélohan and Labbé) composed of coccidin (Labbé). These ultimately are large and round (Figs. 30-32) and are refractile in fresh preparations, where they appear yellow or greyish-green. They tend to shrink in preparations fixed with sublimate or sublimate acetic (Fig. 29). The plastinoid granules occur between and among the chromatoid granules (Figs. 30-32). In stained preparations¹ the granules are best seen by staining with iron-hæmatoxylin followed by Van Gieson's picro-fuchsin, when the chromatoid granules appear blackish, while the plastinoid granules take on a uniform, yellowish hue. The plastinoid granules stain with lichtgrün in marked contrast with the red of safranin taken up by the chromatoid granules. With Delafield's hæmatoxylin, the chromatoid granules stain intensely (Figs. 29, 31, 32) and somewhat misleading appearances result, suggesting multiplication of the cell.

As the parasite grows, the chromatoid and plastinoid granules travel towards the periphery (Figs. 29-32). The macro-gametocyte at this time encysts within the epithelium, and the chitinous material of the cyst seems to be formed from the chromatoid granules. At any rate, the inner layer of the cyst-wall seems to take its origin therefrom (Figs. 34-36). The formation of the cyst-wall from the chromatoid granules has been noted by Simond (1897) and Wasielewski (1904) in the case of *Coccidium oviforme* (*Eimeria stiedæ* of Stiles).

The formation of the cyst of *Eimeria avium* takes place while the organism is still within the epithelium (Figs. 34, 35), and therefore the parasite encysts precociously. The macrogamete at this stage is ovoid, and the number of chromatoid granules within it is reduced. The cyst formed is ultimately rather thick-walled, but a small aperture or micropyle, which may be in a slight depression, is left for the entry of the microgamete (Pl. xxxvi., Fig. 47).

When Schaudinn investigated the life-cycle of *E. schubergi*, he described a process of maturation of the macro-gametocyte, whereby the karyosome of the nucleus was expelled in fragments. I regret that I am not at all sure as to the fate of the karyosome of the macro-gametocyte of *E. avium*. Several causes combine to defeat the attempts made to elucidate this subject. In the first place,

¹ The reactions of the granules are discussed by Labbé (1896) and by Minchin (1903).

PLATE XXXVI.



H.B. Pantham del.

E. Wilson, Cambridge

EIMERIA (COCCIDIUM) AVIUM.
(Microgametes, Sporogony.)

the entire parasite (*E. avium*) is much smaller than *E. schubergi*, and its karyosome is not nearly so well differentiated a structure. Further, the presence of the chromatoid granules, which stain deeply with basic stains, much confuses the structure. Similar causes prevail in *E. oviforme* (*E. stiedæ*), as I can vouch from personal observation, and Wasielewski (1904, p. 54) states that he is unable to follow the maturation process in *E. oviforme*.

It may be that *E. avium* is like some other Coccidia (e.g., *C. lacazei* *C. proprium*, *Adelea ovata*) where the karyosome is retained in the gamete and is left behind in the residual protoplasm of the oöcyst. On a few occasions, I have observed a small chromatin-like granule in the oöcyst residuum (Pl. xxxvi., Fig. 57), and this body may be the karyosome of the macro-gametocyte. *E. avium* is distinguished by having a very small cystal residuum, which, together with the smallness of the karyosome, and indeed of the whole parasite, increases the difficulty of investigation. However, at the time of fertilisation, the distinctness of the karyosome of the macrogamete has disappeared (Pl. xxxv., Figs. 29-36), and the nucleus of the macrogamete appears to contain granules of chromatin which are rather indistinct.

The micro-gametocyte¹ (Pl. xxxvi., Fig. 37) is an ovoid cell about 13 μ long and 8 μ broad in the specimens that I have seen. It possesses a central nucleus containing a karyosome. The process of the formation of the microgametes of *E. avium* is as follows:—The chromatin of the nucleus, largely concentrated in the karyosome, breaks up (Figs. 38-40) into minute granules or chromidia which pass towards the surface of the cell, where they appear to form a *very* fine chromidial network (Fig. 38). The chromidia then collect into groups or patches, arranged in the form of minute, irregular loops with central hollows (Figs. 38, 39). These chromatic loops form a number of minute, flexible, rod-like bodies, composed almost entirely of chromatin (Figs. 41-45). These are the young microgametes (Figs. 43-46). The adult microgametes are small parasites, their chromatic bodies measuring 3 μ to 4 μ in length, possessing a rod-like, somewhat curved body composed of a core of chromatin, which is surrounded by a tenuous film of cytoplasm, prolonged outwards to form two fine flagella (Figs. 44, 46). The flagellum, which I term the posterior flagellum, trails behind the organism, and is practically a continuation of its body; the other flagellum is at the opposite end of the body, and so is termed the anterior flagellum. In life, the microgametes are capable of serpentiiform movements. Owing to the minute size

¹ Uni-nucleate micro-gametocytes seemed rare in preparations, for the cell rapidly proceeds to form many microgametes.

Micro-gametocyte and micro-gametes.

of the microgamete (about 3μ to 4μ long) it is only with the greatest difficulty that the flagella can be discerned.

The whole of the micro-gametocyte is not used in the formation of the microgametes. When separation of the microgametes from their mother cell occurs, a large amount of the body-substance of the latter remains as a somewhat faint staining residuum, in which the pale staining remains of the karyosome (Fig. 43, *cf.* Fig. 38) can sometimes be distinguished. The residuum takes no further part in the vital activities of the parasite.

The microgametes are set free into the lumen of the gut, and proceed to seek out the macrogametes.

When the macrogamete has attained its maximum development, it often lies in the epithelium, near the outer edge of the tissue, or may even burst through the attenuate wall of the host-cell and so reach the margin of the lumen of the gut. The minute but active microgametes (Pl. xxxvi., Fig. 46) meanwhile have broken away from the residual protoplasm of the host-cell, and swum out with rapid lashing movements of their flagella into the gut. Here they are attracted, possibly by some chemiotactic substance, towards the macrogametes. The microgametes swarm round the micropyle of the macrogamete (Pl. xxxvi., Fig. 47¹) and several have been seen trying to enter it simultaneously. The nucleus of the macrogamete travels upwards nearer the micropyle, and before long one microgamete effects an entry (Fig. 47¹), appears to bore its way into the female, reach the nucleus, and finally be lost to view. The macrogamete secretes a plug of protoplasm across the micropyle, whereby other microgametes are excluded, and the individuals thus shut out degenerate (Fig. 48). Such is the process of conjugation as seen in the living organism, and the evidence of stained preparations is fully confirmatory of what has just been described.

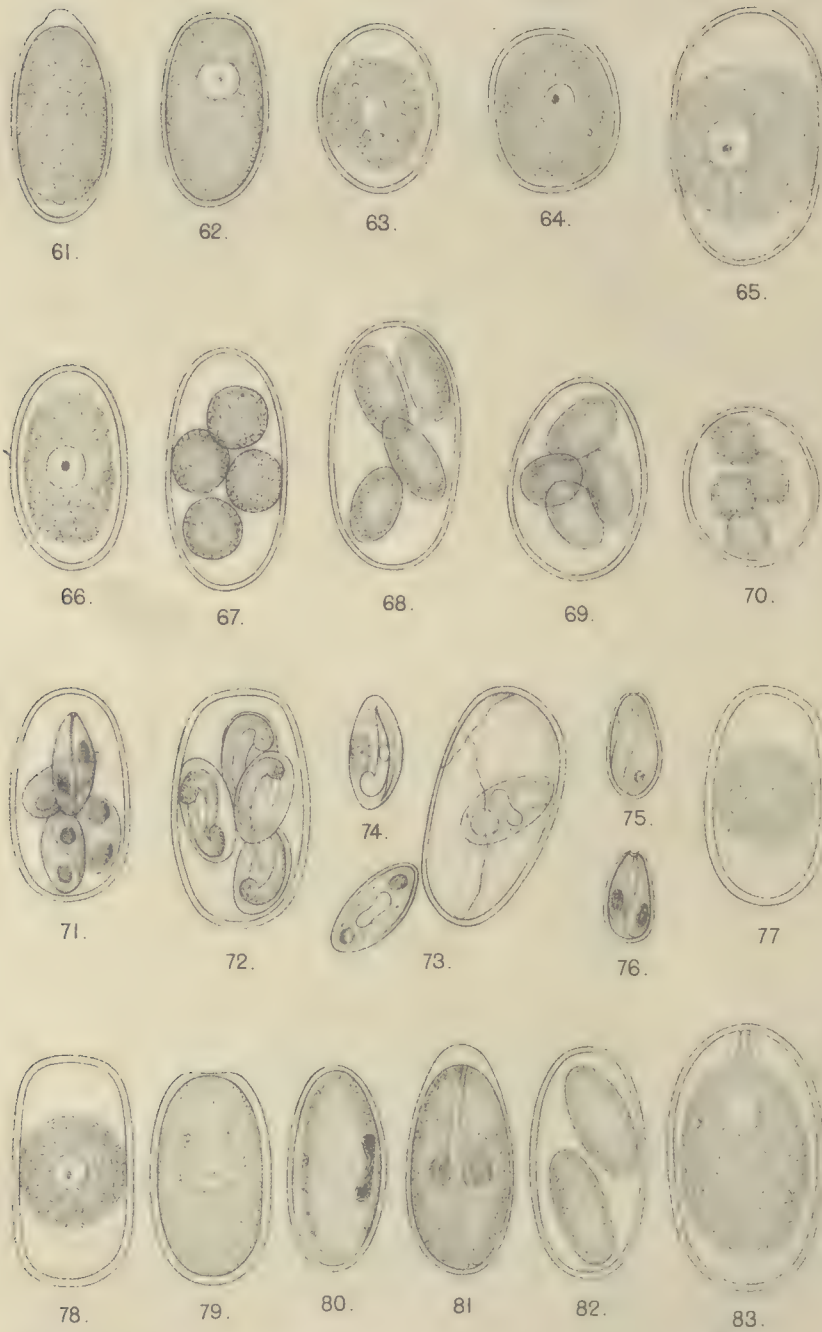
Owing to the presence of granules in the macrogamete it is extremely difficult to follow the subsequent stages of fertilisation. Occasionally there are indications of a fertilisation spindle (Figs. 50, 51), but the nature of the material frequently precluded observation of the same.

The term "fertilisation spindle" is not exactly a happy one, for the object of that structure is the intimate intermingling of the chromatin of the uniting gametes.

After the microgamete has reached the nucleus of the macrogamete, fusion

¹ See also Pl. xxxviii., Fig. 3, p. 252.

PLATE XXXVII.



H B Fartham, del.

E Wilson, Cambridge.

EIMERIA (COCCIDIUM) AVIUM
(Sporogony.)

occurs and a zygote is produced. The contents of the zygote at first fill the oval oöcyst (Pl. XXXVI., Figs. 49-52), but gradually they shrink away from the poles.¹ The oöcyst itself may increase slightly in size during the con-^{Sporogony.}centration of its contents, which ultimately form a globular mass, consisting of cytoplasm rich in fatty matters, within which is a nucleus, usually centrally placed.

The nucleus (synkaryon) of the zygote proceeds to divide directly, first into two (Figs. 53, 56) and then into four (Fig. 54), the divisions following one another very rapidly. The granular protoplasm segments around the nuclei, and four sporoblasts (Fig. 57) are produced, each sporoblast separating from its neighbours as a small, rounded body (Figs. 55-57). Occasionally oöcysts containing two ovoid masses of protoplasm (Pl. XXXVII., Fig. 82) are seen, but as a rule the form containing four sporoblasts is the one found, the four sporoblasts being formed almost concurrently. The sporoblasts become ovoid (Pl. XXXVI., Fig. 58; Pl. XXXVII., Fig. 68), and each gradually secretes a tough, chitinous sporocyst, usually differentiated as epispore and endospore, and so becomes a firm, resistant spore (Pl. XXXVII., Figs. 71-76). A minute amount of the cytoplasm of the zygote is not used in spore formation, but remains within the zygote as a small crystal residuum.

The sporocysts continue within the oöcysts for some time, during which period each sporocyst undergoes developmental changes, leading to the production of actively motile sporozoites. The contents of the spore at first are homogeneous (Pl. XXXVII., Figs. 68-70), but gradually two refractile bodies or vacuoles appear at either end (Fig. 73), and the protoplasm gradually concentrates into two masses, just internal to each vacuole. The nucleus is at first central, but divides into two, and the halves migrate to the opposite poles of the sporocyst (Pl. XXXVI., Fig. 58). The protoplasmic masses gradually displace the polar vesicles, so that the two vacuoles move towards the centre and coalesce (Pl. XXXVII., Fig. 73), leaving nearly all the protoplasm of the sporocyst in two masses, one at each end (Fig. 71). Each of the protoplasmic masses gradually becomes vermiform, extending along one edge of the spore (Figs. 71, 72). Two vermiform sporozoites are thus formed (Figs. 72, 74), sometimes with their more rounded ends placed at opposite ends of the sporocyst (*tête-bêche*) (Figs. 72, 74, 75), sometimes with the slightly swollen ends side by side (Pl. XXXVI., Fig. 59; Pl. XXXVII., Fig. 76), the sporozoites being capable of movement within the spore just previous to their escape. There is a slight sporal residuum.

¹ In some cases the zygote-contents of the oöcyst may be slightly nearer one pole than the other.

The sporocysts when quite ripe tend to become more pointed at one end (Pl. xxxvi., Fig. 60; Pl. xxxvii., Figs. 71, 75, 76), where a slight thickening or small Stieda's plate (Fig. 71) may appear, which is a point of weakness, for here a rupture may occur under the action of the digestive juices of the fresh host, forming a sort of micropyle through which the sporozoites escape. Partially ruptured sporocysts are sometimes found (Pl. xxxvi., Figs. 59, 60). In the case of Grouse chicks dying from acute Coccidiosis, ripe sporocysts have been found in the cæcal walls themselves, as well as in the cæcal contents, though usually mature sporocysts are found in cæcal droppings that have been exposed.

The oöcysts of *Eimeria avium* show a fair amount of variation among themselves. Usually the oöcysts are oval (Pl. xxxvii., Figs. 65-68, 71, 72, 77, 78), actually measured specimens varying from 25μ to 35μ in length and from 14μ to 20μ in breadth. Sometimes the oöcysts are not oval but subspherical (Fig. 70), and these are from 18μ to 20μ in diameter. Somewhat pyriform or egg-shaped oöcysts (Fig. 69) are intermediate in size between the oval and subspherical forms. Morse (1908) noted the occurrence of both round and oval oöcysts when investigating white diarrhœa of fowls, in which Coccidiosis played an important part.

Among the oöcysts of *E. avium* certain were found with somewhat squarish ends (Fig. 78), while others had a slight depression at the apex (Fig. 79), but their development was identical with that of the more common forms. Occasionally, oöcysts with two sporocysts only (Figs. 81, 82) were found, but these were abnormal forms, as was also a parasite (Fig. 83) in which the cytoplasm extended in a cone or funnel-like fashion to the edge of the oöcyst.

The size and shape of the oöcysts are largely determined by the space in which the macrogamete develops and the amount of food available for the parasite. When there are many *Eimeria* present in any particular region of the gut, the oöcysts produced are relatively small, while where abundance of space and nourishment are available, the oöcysts tend to be large.

From experiments made by feeding birds with cœcidian oöcysts, I conclude that schizogony takes from four to five days. Uni-nucleate oöcysts mature their sporocysts in two to three days. The period for the total life-history of the parasite would be from eight to ten days.

The larvæ and imâgines of *Scatophaga stercoraria*, the dung-fly, ingest the oöcysts of *E. avium* along with the Grouse fæces. The oöcysts pass through the bodies of the larvæ uninjured, and are scattered with the excrement, thus serving to disperse the spores to some extent.

IV. SUMMARY OF THE LIFE-HISTORY OF *EIMERIA AVIUM*.

The life-cycle of *Eimeria avium* is complicated, even though the organism completes its development within one host. The life-history may be represented diagrammatically as in Text-Fig. 1, A-T (p. 248). Beginning as a sporozoite (Pl. xxxiv., Fig. 2; Text-Fig. 1, A) liberated by the action of the pancreatic juice of the Grouse, the parasite rapidly penetrates an epithelial cell of the duodenum (Text-Fig. 1, B) and entering the cell rounds up (Text-Fig. 1, C) and becomes a passive growing trophozoite (Pl. xxxiv., Figs. 3-7; Text-Fig. 1, D). After a period of rapid growth, during which time the trophozoite (Figs. 8-11) practically destroys the cell harbouring it, the parasite enters upon an asexual, multiplicative phase termed schizogony.

The schizont is at first uni-nucleate (Fig. 12; Text-Fig. 1, D) but the nucleus soon fragments (Figs. 12, 13), the daughter nuclei migrate to the periphery (Figs. 14-16; Text-Fig. 1, E), cytoplasm segregates around each (Text-Fig. 1, F), and the daughter forms thus produced become meridionally arranged, like the segments of an orange, the arrangement of the merozoites being "en barillet" (Pl. xxxiv., Figs. 17-22; Pl. xxxv., Figs. 23-25; Text-Fig. 1, G).

Each merozoite is a small, vermicular organism, having a nucleus with a somewhat ill-defined karyosome usually to one side (Fig. 24). The groups of merozoites break up (Text-Fig. 1, H), and the free germs seek out and enter an hitherto uninfected cell where the parasite again assumes the trophic phase and then undergoes division as before. Several successive generations of schizonts and merozoites are thus produced, resulting in a great destruction of the gut-epithelium of the host. Finally a limit is reached to the ability of the host to provide nourishment and to the multiplicative powers of the parasite, and this results in the onset of sexual differentiation. Gametogony may occur both in the duodenum and cæcum.

Certain schizonts become considerably modified in one of two directions. In the first case, food material accumulates, and a large, uni-nucleate food-laden form is produced (Figs. 26-30). This is the macro-gametocyte (Text-Fig. 1, I ♀), destined to give rise to a single macrogamete (Text-Fig. 1, J ♀). In the second instance (Text-Fig. 1, I ♂), nuclear multiplication of a finely granular parasite (Pl. xxxvi., Fig. 37) occurs, and the many minute nuclei produced reach the periphery of the host-cell (Figs. 38-42), and ultimately the now multi-nucleate micro-gametocyte (Text-Fig. 1, J ♂) gives rise to a large number of small, motile microgametes (Figs. 43-46; Text-Fig. 1, K ♂). The macrogamete early invests itself with a cyst-wall (Figs. 35, 36) in which a thin part or micropyle is left for the entry of the microgamete

TEXT-FIG. 1.

- A. Sporozoite which penetrates epithelial cell of the duodenum of the host.
 B. Sporozoite curving on itself before becoming rounded within the host-cell.
 C. Young, uni-nucleate trophozoite.
 D. Fully grown trophozoite or uni-nucleate schizont.

- E. Schizont with numerous daughter nuclei peripherally arranged, differentiating to form merozoites (seen in transverse section).
 F. Schizont showing further differentiation of merozoites (seen in oblique section).
 G. Merozoites arranged "en barillet,"

- about to issue from host-cell.
 At one end of the cluster residual protoplasm is seen.
 H. Free merozoites, each with a small karyosome.

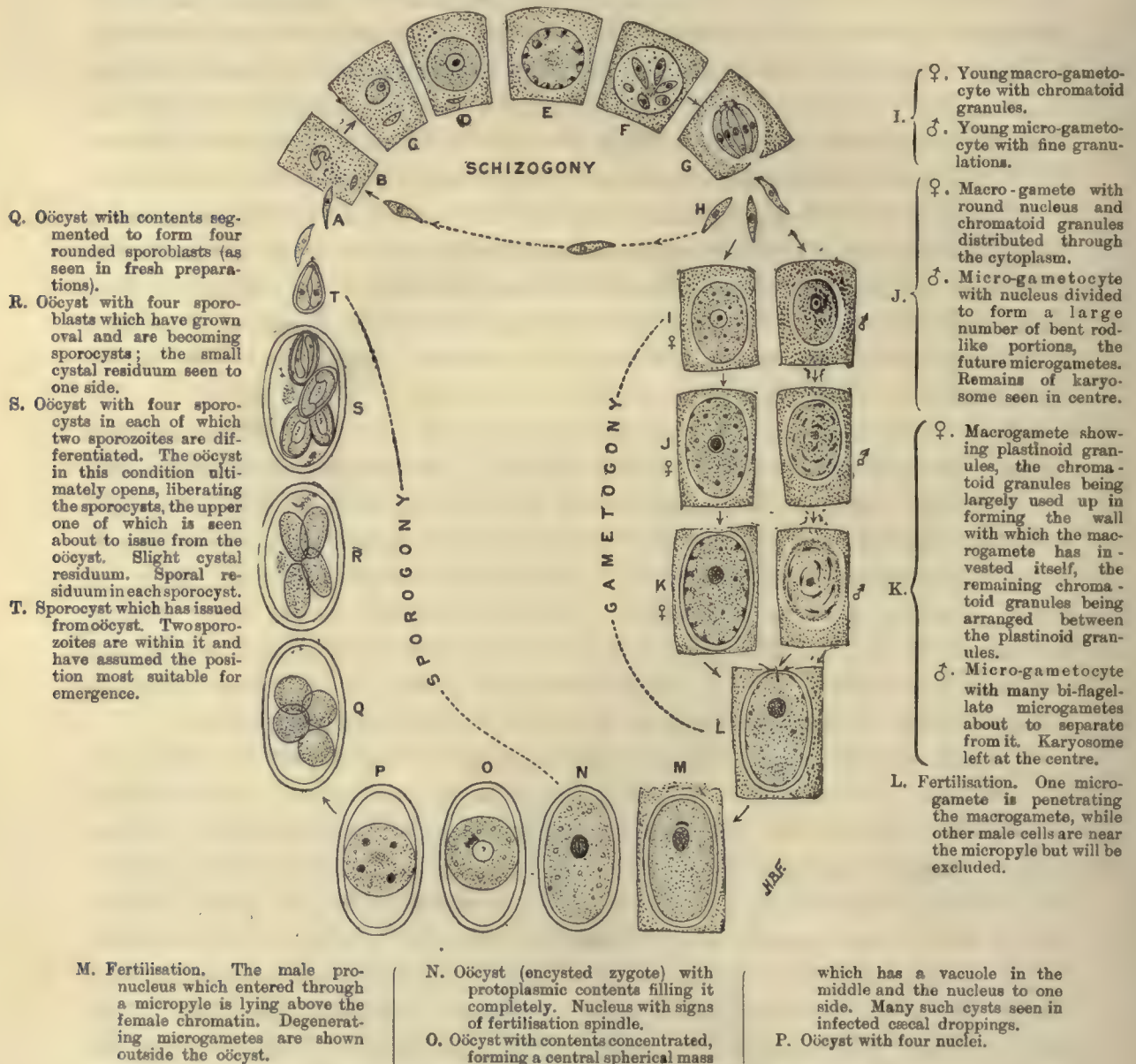


Diagram of Life-cycle of *Eimeria (Coccidium) avium*.
 D-H represent Schizogony. I-L, Gametogony. N-T, Sporogony.
 Epithelial host-cells diagrammatically outlined.

(Pl. xxxvi., Figs. 47, 48 ; Text-Fig. 1, K ♀). This oöcyst-wall is formed while the parasite is within the epithelium.

Fertilisation (Figs. 47, 48 ; Text-Fig. 1, L) occurs—the process has been watched in life—and the micropyle is then closed (Figs. 49-51 ; Text-Fig. 1, M). The fertilised oöcyst (Text-Fig. 1, N) then passes into the lumen of the gut and is voided with the fæces of the Grouse. The further development of the oöcyst largely depends on climatic conditions. Under the influence of warmth and moisture, the contents of the oval oöcyst (Pl. xxxvi., Fig. 52 ; Pl. xxxvii., Figs. 61, 62, 64) shrink away from the poles and become a rounded, central mass (Figs. 65, 77, 78 ; Text-Fig. 1, O). The nucleus rapidly divides into two (Pl. xxxvi., Fig. 56) then four (Fig. 54 ; Text-Fig. 1, P) ; each nucleus has protoplasm segregated around it (Pl. xxxvi., Fig. 55 ; Pl. xxxvii., Figs. 67, 70 ; Text-Fig. 1, Q), a wall is secreted, and the net result is that four sporocysts (Figs. 58, 71-76 ; Text-Fig. 1, R) are produced within the oöcyst. Within each sporocyst two sporozoites gradually differentiate (Figs. 58-60, 71-76 ; Text-Fig. 1, S), and when the sporocyst (Text-Fig. 1, T) is ingested by a new host, the sporozoites creep out of the sporocyst softened by the pancreatic juice of the new host and proceed to attack the epithelium of the gut, producing thereby the primary infection of the bird.

The main differences between *Eimeria avium* (Silvestrini and Rivolta) and *E. schubergi* (Schaudinn) may be briefly summarised :—

- (1.) *E. avium* is smaller than *E. schubergi*.
- (2.) The merozoites of *E. avium* are arranged "en barillet," those of *E. schubergi* "en rosace."
- (3.) Precocious encystment of *E. avium* occurs before fertilisation. This is not the case with *E. schubergi*.
- (4.) Fertilisation in *E. avium* is micropylar ; in *E. schubergi* a cone of reception is formed by the macrogamete.
- (5.) The macrogamete of *E. avium* contains much more deeply staining reserve food-material than that of *E. schubergi*, thereby increasing the difficulty of minute examination of the parasite.
- (6.) The cysts of *E. avium* are oval, those of *E. schubergi* are round.

V. THE EFFECT OF *EIMERIA AVIUM* ON THE HOST.

The effect of Coccidiosis on the Grouse may now be considered briefly, fuller details regarding the symptoms of the disease and its effects being given in the article relating to experimental Coccidiosis.¹

¹ Vide Part II. p. 252.

External Effects.—The chief external evidence of Coccidiosis is the pale colour and great fluidity of the cæcal (soft) droppings of the Grouse, the pale tint being due to myriads of oöcysts and the condition being that of diarrhoea. A similar disease in fowls is known among poultry-men as “white-diarrhoea.” As the coccidian parasites cause great denudation of the intestinal epithelium, digestive derangements are brought about, and consequent on this, malnutrition occurs and the bird becomes very emaciated and “anæmic.” Feathering also is poor and ragged, leg weakness is fairly common, and a peculiar bluish tint is sometimes seen at the cere, ears, and other parts.

Eimeria avium appears to be purely a parasite of the gut of the Grouse and does not affect such gut diverticula as the liver. The crop and gizzard of infected birds are rarely parasitised, though they may contain oöcysts in the condition in which they have been ingested with food. Examination of the duodenum shows that the sporocysts ingested with the food are attacked by the pancreatic juice (as I have proved by pancreatic digestion experiments, using both natural pancreatic juice and trypsin), and the sporozoites are set free. These invade the tissue of the duodenum, rapidly become schizonts and multiply, the result being that the duodenum is often riddled by the parasites, and consequently inflamed. Both the villi and the crypts of Lieberkühn are attacked, and the parasites have also been found, though much more rarely, in the submucosa. Great hypertrophy followed by atrophy of the epithelial host-cell occurs, and the tissue attacked is often reduced to a finely granular, structureless mass. Desquamation of the gut is common, and epithelium containing various developmental stages of the parasite can be found floating free in the gut contents.

Some of the merozoites formed in the duodenum pass down the gut, reach the cæca and re-commence their life-cycle there. Active schizogony and sporogony go on in the cæca,¹ chiefly in the epithelium, very rarely in the submucosa. Often the cæca are as heavily parasitised as the duodenum, whole areas being completely denuded of the epithelium, especially when the fertilised oöcysts pass outwards into the cæcal contents. The walls of the cæca are often rendered very thin and tender by the action, direct and indirect, of the parasite. Ripe oöcysts and sporocysts occur in the lumen of the cæca of dying chicks.

Podwyssozki (1890) stated that he found coccidian oöcysts in the vitellus of eggs of fowls, especially in summer. He considered it possible that the cysts

¹ Coccidiosis may sometimes occur along the entire length of the small intestine, and gametes may be formed far forward, in the duodenum.

were derived from *Coccidia* in the oviduct of the mother, or perhaps from intestinal *Coccidia* which had ascended by way of the cloaca. I think that cloacal contamination was the more probable, for I have never seen *Coccidia* in the genitalia of adult Grouse examined.

A reflex of Coccidiosis is seen in the blood of infected birds, where polymorphonuclear leucocytosis is induced (*vide* chapter xiii. p. 315).

Lesions caused by *Coccidia* in the mucous membrane may admit bacteria to the circulation of the host (*vide* chapter xii. pp. 295 *et seq.*). Rettger (1909) believes that "white diarrhoea" of fowls in America is due to a bacterium, while Morse (1908) considers that it is primarily due to Coccidiosis. The discrepancy between the results of these American workers is thus capable of explanation.

VI. CONCLUDING REMARKS.

Eimeria avium of Grouse is not restricted to this particular bird, for by administering faeces containing oöcysts from diseased Grouse to young fowl chicks and pigeons, I have been able to reproduce the disease exactly as it occurs in Grouse (p. 254). M'Fadyean (1894) found Coccidiosis in pheasants, while "white diarrhoea" of fowls has been the subject of much investigation, particularly recently in America, where Morse (1908) and Hadley (1909) have worked on the subject. Morse's account of preventive measures is very good, and he also notes Coccidiosis in many other birds, but the figures of the complete life-cycle of the parasite are not yet published. Labbé (1896) also has described Coccidiosis in certain marine birds.

Though Coccidiosis is peculiarly fatal to Grouse chicks during the first few weeks of their lives, adult Grouse also can become infected, for I have examined an adult bird that probably died of Coccidiosis. Old birds in the chronic condition serve as reservoirs of oöcysts and so may form sources of new infections on the moors. All infected corpses should be burned, *not* buried.

I may add that, while correcting the proofs of this memoir, I have been able to examine pheasant chicks dying from Coccidiosis, the birds being obtained through the courtesy of Drs Shipley and Hammond Smith from various parts of England during June and July 1910.

The economic importance of Coccidiosis in birds, especially in the young, is evident, and I trust that this work, which to the best of my belief is the first fully illustrated and detailed life-history of an Avian *Coccidium*, may draw more attention to a subject both of great scientific interest and of practical importance.

PART II.—EXPERIMENTAL STUDIES ON AVIAN COCCIDIOSIS, ESPECIALLY IN
RELATION TO YOUNG GROUSE, FOWLS, AND PIGEONS.

I. INTRODUCTION.

Protozoal parasites are highly specialised animalcules which live in intimate relation with the hosts they infect. While many of the protozoa are capable of living in one host only, there are others which are under suspicion of infecting several species of higher organisms as host, and of not being so limited to one host as was formerly believed. One test for the specificity of any protozoal parasite is that it fails to develop in any animal other than its special, natural host, and merely perishes when inoculated or otherwise introduced into any other animal. In order to test the specificity of the coccidian parasite of the Grouse, experiments were made, with the result that the *Coccidium* pathogenic to young Grouse and responsible for the dwindling of the broods, particularly in the spring and early summer, was found to be equally injurious to healthy young fowls and young pigeons. Healthy Grouse chicks also were experimentally treated by administering food mixed with small quantities of infected fæces from other Grouse suffering from Coccidiosis, and fatal results ensued.

The results set forth in this Memoir are those obtained from one season's work only, to which my investigations were limited.

II. EXPERIMENTAL METHODS.

The birds used in experimental Coccidiosis were Grouse chicks, fowl chicks and young pigeons, all of which were initially healthy. Coccidian oöcysts (Pl. xxxviii., Figs. 4, 5) contained in caecal droppings from infected Grouse were allowed to develop spores to some extent by being thinly spread in Petri dishes and covered in order to prevent complete drying. Under these conditions the spores (Figs. 6, 7) developed in two to three days at summer temperature. The fæces so prepared were then administered to the healthy young birds.

(A) *Grouse Chicks*.—As these birds are somewhat wild, even though bred in captivity, a rapid feeding method was adopted. Some of the partly dried faecal matter was taken up on a spatula and inserted directly into the mouth of the bird. Rather large quantities were given as first doses, but if infection was not fairly rapidly brought about the dose was repeated. The caecal droppings of treated

PLATE XXXVIII.



AVIAN COCCIDIOSIS.

chicks were collected each morning, for these soft droppings are more abundant during the night than they are during the day, and in the early morning there is a better chance of obtaining excrement free from soil. Examination of fæces collected in the evening was sometimes made.

The Grouse chicks were kept on the experimental ground at Frimley, and the feeding experiments were conducted by Dr E. A. Wilson. Samples of the fæces of the birds were sent to me daily.

(B) *Fowl Chicks and Young Pigeons*.—A method of feeding similar to that used for Grouse chicks was employed with fowl chicks and young pigeons (squabs). These experiments were conducted by me at Cambridge. The chicks used were from incubated eggs, the eggs having been carefully cleansed antiseptically before incubation. Cæcal droppings containing oöcysts were administered directly to the birds. Very small daily doses were used for several days and then none for a couple of days, and so on. This method of administering oöcysts was quite effective, and had the advantage of reproducing somewhat the condition of wild Grouse on the moors, where intermittent ingestion of oöcysts with food or drink occurs.

One experiment was performed in which a single dose only had a fatal effect on a fowl chick.

Droppings containing oöcysts in different stages of development (Figs. 4-7) were also used. When the oöcysts contained developed sporocysts the onset of Coccidiosis was more rapid.

Again, I have found coccidian oöcysts in the water of tarns at which Grouse chicks drink and also in dew collected from the heather on the moors (Fig. 8). Grouse chicks, then, can acquire coccidian oöcysts by way of their drink. To show this method of infection experimentally, a healthy fowl chick was supplied with water containing coccidian oöcysts. This bird also became infected with Coccidiosis.

Control birds were most carefully kept. These were supplied with food and drink exactly as were the treated birds, and kept under the same conditions. Examination of their fæces was made twice daily, and careful search was made for oöcysts as the possibility of natural Coccidiosis of both fowls and pigeons¹ was well recognised and most carefully guarded against. Control birds were invariably healthy, and made more rapid progress in growth than did the subjects of the experiment.

¹ Through the courtesy of a friend I was able to examine coccidian oöcysts from a pigeon suffering from natural Coccidiosis. On Pl. xxxviii., Fig. 13 is drawn a cyst of this Coccidium (*C. pfeifferi* of Labbé). It is spherical, about 17μ in diameter.

In every instance I most carefully compared the results obtained experimentally with the cases of natural Coccidiosis in Grouse chicks that I investigated on one of Lord Lovat's moors in Inverness-shire, and in other cases obtained from Perthshire, Dumfriesshire and Yorkshire.

Some authors have given the name *Coccidium cuniculi*¹ to the parasite of birds, thereby identifying the Coccidium of birds with that of rabbits. Having had the opportunity of obtaining fresh material from rabbits dying rapidly of acute Coccidiosis, I fed a healthy young pigeon directly with oöcysts of *C. cuniculi*. At first oöcysts were voided by the pigeon, then none were found in the fæces, and no symptom associated with Coccidiosis appeared at any time. The first oöcysts voided were merely those supplied to the bird which had passed unchanged through its alimentary tract. Though this pigeon received several doses of the oöcysts of *Eimeria* (*Coccidium*) *cuniculi*, it never developed Coccidiosis, and the *post-mortem* examination made immediately after killing the bird showed a perfectly normal condition of every organ. I consider that these experiments show conclusively that *E. avium* and *E. cuniculi* are distinct species of *Eimeria* and are not identical. There are also morphological differences between the two, chiefly of size (*E. avium* is the smaller).

III. SYMPTOMS OF COCCIDIOSIS.

The symptoms of Grouse suffering from natural Coccidiosis and those of Grouse, fowl chicks, and pigeons, in which the disease has been artificially induced, are identical. The symptoms that have been noted in the case of the birds examined may now be stated.

Chicks after ingesting coccidian oöcysts become far less active in their movements as a rule. The first noticeable feature is the drooping of their wings and a habit of constantly looking downwards. The birds stand about more than normal birds, and their calls are more plaintive.

While fowl chicks and pigeons appear to mope, their appetite is increased, and chicks experimentally infected with Coccidiosis eat far more greedily than the control birds. They also drink considerably more. In spite of the increase in the amount of food consumed, the birds rapidly get thinner, the muscles of the breast and legs showing this to a marked degree. Throughout the progress of the disease the growth of the affected birds is much retarded.

It was necessary to feed infected young pigeons by hand, for even when they

¹ The correct name of this parasite is *Eimeria stiedæ* Lindemann.

reached practically adult life they failed to feed themselves, merely thrusting their heads into the food offered them, without attempting to swallow any of it.

Several breeds of fowl chicks were used in experimental Coccidiosis, and each lost weight steadily till death occurred. The loss of weight of one pure bred Leghorn chick was very noticeable. It was first fed with coccidian oöcysts when six weeks old. It and its control bird were then of equal weights ($7\frac{1}{2}$ oz.). Two months later the infected chick died, its weight at death being 5 oz., while the weight of its control on the same day was 1 lb. 6 oz.

Sample weights of other experimental birds are given below :—

BIRD.	Weight of Infected Bird.	Weight of Control Bird.	Difference in Weights.	REMARKS.
Grouse chick A . . .	4 oz.	$5\frac{1}{2}$ oz.	$1\frac{1}{2}$ oz.	Dosed once when 11 days old. Killed <i>in extremis</i> when aged 6 weeks. Died, aged 10 weeks.
Grouse chick B . . .	$4\frac{1}{4}$ oz.	7 oz.	$2\frac{3}{4}$ oz.	
Grouse chick C . . .	$6\frac{1}{2}$ oz.	9 oz.	$2\frac{1}{2}$ oz.	
Minorea hen . . .	3 lb. 2 oz.	5 lb. 2 oz.	2 lb.	Died, aged 6 months.
Plymouth Rock cock .	4 lb. 8 oz.	6 lb. 5 oz.	1 lb. 13 oz.	Killed, at acute stage of disease. Chronic.
Cross-bred Leghorn .	4 lb. 10 oz.	5 lb. 4 oz.	10 oz.	
Pigeon	$9\frac{1}{2}$ oz.	12 oz.	$2\frac{1}{2}$ oz.	Died, aged 11 weeks.

NOTE.—The three fowl chicks were first treated with coccidian oöcysts when aged three weeks. Another fowl chick fed with coccidian oöcysts when aged one day, died when nine days old. The pigeon squab was dosed first when aged nine days.

Another instance of loss of weight resultant on Coccidiosis was seen in the case of a pure bred female Leghorn chick which was attacked when seven weeks old by Coccidiosis after drinking water fouled with coccidian oöcysts. This bird became “a chronic,” and when adult weighed 4 lb. 3 oz., while its sister bird that acted as control weighed 5 lb. 4 oz.

Besides loss of weight the infected birds become anæmic. The cere, comb, and wattles become much paler and the blood-vessels beneath the wing also look pale. The head appendages gradually become more and more pale as the disease progresses, and finally acquire a peculiar bluish tinge. This tint also is shown by the eyelids and ears, and the legs are affected, though to a less extent. The feathers on the

head tend to fall off so that the forepart of the head and the region round the bill become almost bald, and the bird presents a very peculiar appearance, owing to the bluish coloration. Leg weakness was present in several cases.

The plumage of the infected birds is affected in regions other than the head, and the quills are less rigid than in normal birds. The feathering of the legs is ragged, and the sheen on the neck and tail-coverts is not so well developed, while the replacement of nestling down by ordinary feathers is much retarded in diseased birds.

During the progress of Coccidiosis the birds sometimes develop much mucus and a very offensive "breath," a smell of sulphuretted hydrogen being noticeable. Both sticky mucus and smell disappear as a rule in a few days, but may recur.

While birds suffering from Coccidiosis feed greedily, internal digestive troubles occur, and the fæces voided by the birds are very fluid, the condition being that of diarrhoea. The cæcal droppings are the more noticeable, and they contain many resistant cysts (oöcysts) (Figs. 4-8) of *C. avium*. Both sportsmen and keepers have noted that diarrhoea is a marked symptom of "Grouse Disease." Examination of soft droppings daily shows the relative numbers of oöcysts present, and may be a rough gauge of the intensity of the infection.¹ In good health the cæcal droppings are of firm consistency and olive-green to brown in colour. When Coccidiosis is slight, the fæces become softer and brownish yellow. In acute cases the excrement is almost fluid, and the birds void sulphur-yellow fæces with a heavy, foetid odour. Fatty matters may be present in the cæcal contents.

A day or so before the death of the infected bird the slimy, mucilaginous discharge recommences, ooze coming from the beak, nares, ears, and eyes. Examination of this liquid by the microscope shows the presence of oval coccidian oöcysts (*cf.* Pl. xxxviii., Figs. 4-8), all of which show the characteristic cyst-wall within which is a single uninucleate mass of protoplasm. The mucus also contains some shed epithelial cells in which occasionally macro- and micro-gametes may be found. The ooze from the eyes and beak chiefly contains oöcysts which may be due to regurgitation from the crop just before death. However, it should be noted that while mucous discharge is common, it is not an invariable feature of Coccidiosis.

Death from Coccidiosis appears to be sudden. Some of the experimental fowl chicks were feeding greedily an hour before death, though death was almost

¹ It should be noted that in severe cases of duodenal Coccidiosis, merozoites may be found free in the gut contents and fæces of infected birds when no oöcysts are present.

expected from the great emaciation and "bluish" appearance of the birds for some days previous to the actual decease.

All infected corpses should be burned, *not* buried.

IV. INTERNAL ORGANS.

Detailed examination of diseased birds shows that Coccidiosis of fowls, pigeons, and young Grouse is confined chiefly to the digestive tract, and so is unlike the Coccidiosis of the rabbit, where both the liver and the gut may be affected.

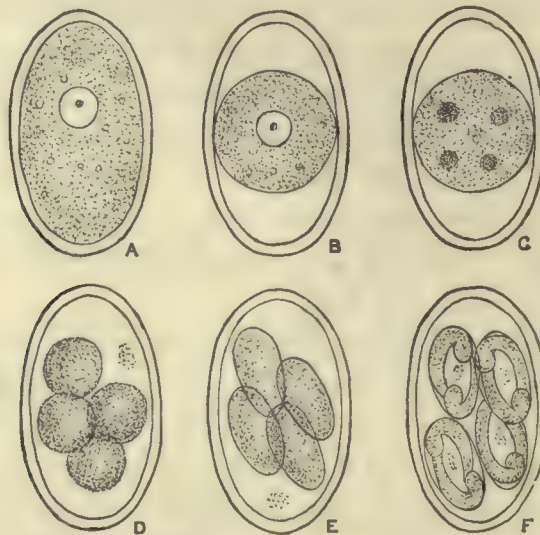
Dead chicks have shown oval coccidian oöcysts (Text-Fig. 2, p. 258) in the discharge from the nostrils. Scrapings from the soft palate, trachea, and oesophagus of diseased birds have shown the presence of oöcysts embedded in mucilage. Possibly the oöcysts may have regurgitated from the gizzard or intestine. Oöcysts are occasionally present in the crop and gizzard, mixed with crushed food, having been probably taken up with the food.

The intestine is more highly parasitised than any other part of the alimentary tract. The oöcysts (Pl. XXXVIII., Figs. 7, 8, 11, 12), which show much variation among themselves, are softened by the pancreatic juice, the four sporocysts (Figs. 9, 10) emerge, and from each of them two active, motile sporozoites or germs come out and proceed to attack the epithelium of the duodenum. Having penetrated the epithelium (Fig. 1) they become round, grow and produce individuals, destined to divide and give rise to a barrel-shaped mass of active daughter germs, the merozoites (Fig. 1, *mz*). These merozoites separate from one another and infect fresh epithelial cells, the whole mucous membrane being soon badly infested, and becoming reduced to an almost structureless mass (Fig. 1). Owing to heavy infection in the duodenal epithelium, death of the young Grouse may occur. However, in many cases, some of the merozoites pass into the lumen of the gut and reach the cæca, the tissues of which are similarly mutilated. As far as my experiments go at present, the full period of schizogony would appear to be from four to five days, as judged by the appearance and general moping of the birds.

After several generations of merozoites have been produced, the power of the host to provide food for the parasite fails, and consequent on this, the latter begins to make preparation for extra-corporeal life, and produces large, granular forms, which are female (mother) cells or macro-gametocytes (Fig. 1, ♀) and somewhat smaller, less granular ones which are micro-gametocytes (Fig. 2, ♂). Each macro-gametocyte gives rise to one passive macrogamete or female element (Fig. 1), while

each micro-gametocyte gives rise to many minute, motile microgametes, the male elements (Fig. 2). Fertilisation (Fig. 3) occurs through a micropyle left in the wall with which the macrogamete invests itself, and the fertilised oöcyst so produced, passes out through the much damaged epithelium into the lumen of the gut and thence to the outside. The epithelium of the duodenum and cæca is sometimes

TEXT FIG. 2.



FIGS. A-F.

Stages in the development of the oöcysts of *Eimeria avium*, as seen in fresh preparations.

- A. Oöcyst (encysted zygote) with protoplasm completely filling it.
- B. Older oöcyst with zygote contents forming a central sphere. Many such oöcysts are found in infected cæca and infected fæces of Grouse.
- C. Oöcyst with four nuclei, about to form sporoblasts.
- D. Oöcyst with four round sporoblasts.
- E. Four ovoid sporocysts within oöcyst.
- F. Fully mature oöcyst with four sporocysts, each containing two sporozoites.

entirely denuded by the action of the many parasites that infest it, and the sub-mucosa also is sometimes infected by the *Eimeria*.

The contents of the oöcyst, at first filling the interior (Text-Fig. 2, A), gradually contract (Text-Fig. 2, B), towards the centre, or occasionally towards one pole, and then divide (Text-Fig. 2, C) into four round masses (Text-Fig. 2, D) known as sporoblasts. Each sporoblast becomes an oval sporocyst (Text-Fig. 2, E) while still within the oöcyst, and within each ripe sporocyst two sporozoites or germs are developed. Consequently each oöcyst gives rise to eight sporozoites (Text-Fig. 2, F).

A certain amount of variation, as exhibited by the oöcysts of *E. avium*, has been noticed by Morse (1908) in the coccidian parasite of "white diarrhoea" of fowls, where the oöcysts are round to oval, and from 12μ to 25μ in diameter. The oöcysts of *E. avium* in Grouse, which is identical with the parasite found in "white diarrhoea" of fowls, also vary among themselves. Usually the oöcysts are oval (Pl. XXXVIII., Figs. 4-8), but a series of varying sizes and shapes can readily be found (Figs. 8, 11, 12, 14), while round oöcysts also occur (Fig. 11). The exact shape and size of the oöcyst is determined by the space in the cell available for the development of the macrogamete, and should not be insisted upon as a specific character, for where many parasites are aggregated together in a limited area of epithelium, the macrogametes and oöcysts are small, while in areas of the gut but poorly parasitised, large oöcysts preponderate. Nutrition of the parasite has obviously a great influence on both its size and its propagative power.

In some cases the gut-wall is extremely thin and tender; in other birds this effect is not marked. Inflammatory patches may be seen at intervals, particularly in the cæca, and the cæca usually are enlarged. At the ileo-cæcal junction, where a recurrence of schizogony and sporogony occurs, much degenerated epithelium is present in the gut contents, and this epithelium contains both schizonts and gametocytes.

The large intestine of chicks infected with Coccidiosis sometimes shows inflammatory patches, and blood may be present in the rectal contents. The rectum itself seems rarely to be attacked by *E. avium*, though its contents usually contain oöcysts.

The kidneys, spleen, liver, and gall-bladder of birds suffering from Coccidiosis never contained *Eimeria*, though the spleen and gall-bladder were sometimes enlarged. Examination of the generative organs has shown no stage of *E. avium* so far, though it is possible that eggs may become contaminated during their passage through the cloaca of the mother. The young chicks then might be hatched in contact with infectious material, and so acquire Coccidiosis early in life. Eight days old Grouse chicks were the youngest naturally infected chicks that I examined. The period of eight to ten days is the one determined roughly by my experiments as being required for the complete developmental cycle of *E. avium* in fowls and pigeons, from the time of ingestion of the oöcysts to the excretion of the maximum number of oöcysts of the second generation.

Many bacteria are present naturally in the gut of the Grouse, and their active movements can be well seen, especially in the cæcal contents of freshly killed

Grouse. Examination of sections of the gut of the Grouse, especially of sections stained with iron-hæmatoxylin and iron-hæmatoxylin followed by Van Gieson's stain, reveals the presence of numerous bacteria, which are present, not only in the lumen of the gut, but forming a layer along the striated edge of the columnar epithelial cells, and also are found in lesions left by the outward passage of gametes and merozoites. These bacteria may have a harmful effect on the tissues invaded, and there is evidence to show that they gain access to the tissues very early, the sporozoites and merozoites acting, in fact, as inoculating needles, whereby the injurious bacteria are passed into the tissue of the gut, whence, by way of the blood and lymph, they can reach other organs. Further, the denudation of the epithelium of the gut allows of easy entry of bacterial agents of infection.

In connection with the action of bacteria in the disease of fowls known as "white diarrhoea," there are two opposing views. Morse (1908), working in America, has investigated white diarrhoea in fowls and other birds, and always found intestinal Coccidiosis. Hadley (1909), also working on the subject, found not only intestinal but also hepatic Coccidiosis in fowls suffering from white diarrhoea. Morse notes the presence of bacteria in the gut, and thinks that they may gain access to the system on account of the denudation of the gut epithelium. Rettger (1909), on the other hand, considers that white diarrhoea is due entirely to a bacterium, *Bacterium septicemix gallinarum* or *Bacterium pullorum*.

Probably both of these conflicting views are right as far as they go, but separately they may only partially explain the cause of "white diarrhoea." Drs Cobbett and Graham-Smith have shown (1910) experimentally that bacteria may be inoculated by means of Coccidia, and find their way into the internal organs probably by way of the portal vein (*vide* chapter xii. p. 295 *et seq.*). The agency of parasitic worms and Coccidia in causing lesions of the mucous membrane through which harmful bacteria may enter is of far-reaching importance, and probably of wide application in the elucidation of certain intestinal diseases.

Morse's paper gives much valuable information regarding treatment of Coccidiosis and brief notes on intestinal Coccidiosis of various birds. Game birds other than Grouse are susceptible to Coccidiosis, for M'Fadyean reported Coccidiosis in Pheasants in 1893-1894. At the time of correcting proofs of this article I am engaged in investigating Coccidiosis which is causing the death of many young Pheasants in various parts of England.

The onset of sporogony of *E. avium* means, as a rule, either the recovery or the death of the infected chick. When the oöcysts pass out from the body of the host,

the epithelium of the gut may be able to recover itself, when the bird gradually increases in weight and makes partial or entire recovery. This recovery is sometimes aided by infiltration of connective tissue into the lesions. If, however, the infection has been heavy, the epithelium cannot regenerate itself, and the bird becomes exhausted and dies.

V. RELATIVE RESISTANCE OF DIFFERENT BREEDS OF FOWLS AND PIGEONS TO COCCIDIOSIS.

Young chicks are far more susceptible to Coccidiosis than adult birds.¹ Very young fowl chicks (up to eight days old) die in a few days after being fed with coccidian oöcysts. Chicks first dosed with cysts when fourteen days old do not succumb so readily; they may live for some weeks, or some may become chronics, when daily examination of their fæces shows periodic small crops of oöcysts.

Older chicks are more likely to recover from Coccidiosis. For example, a Grouse chick aged thirteen weeks was fed on oöcysts, and when killed three weeks later very few Coccidia were observed. Again, a young Grouse which had been picked up dead on the moors in Inverness-shire was received on September 15th, 1909. In its cæca numbers of both coccidian oöcysts and *Trichostrongylus pergracilis* were found. The bird had probably survived an attack of Coccidiosis and in its weakened condition had fallen a victim to Strongylosis.

Different breeds of fowls have varying powers of resisting Coccidiosis. Pure-bred Leghorn and Minorca chicks died from the disease in a comparatively short time. Plymouth Rock chicks were attacked quickly, but had greater resisting powers than pure Leghorns or Minorcas. Cross-bred Leghorns were far more resistant to the disease than the pure-bred birds.

Regarding pigeons, Fantails are more susceptible than the ordinary pigeons, though squabs of any variety seem easily attacked and overcome by Coccidiosis.

VI. THE DISSEMINATION OF COCCIDIOSIS OVER TRACTS OF COUNTRY.

Coccidiosis outbreaks spread with fair rapidity, but though many birds in one locality become diseased, adjoining estates may be free. Epizootics of Coccidiosis also disappear very quickly.

Infection has been shown experimentally to be due to the ingestion of oöcysts (cysts), either by way of the food or drink. Coccidian cysts may occur on the

¹ Old birds may become chronics and thus infect the moors. In this connection infected foster-mothers in Pheasant-rearing may be dangerous.

heather and in the tarns and pools from which the Grouse drink, as before mentioned.

When fæces of infected chicks are voided, the cæcal or soft droppings are heavily loaded with cysts, and not only do they foul the ground, heather, and water in their vicinity, but, when dried, the powdery material produced may be disseminated by the wind, and so oöcysts and their contained sporocysts are distributed over comparatively large tracts of country.

But other methods of producing richer local infections may be partly due to insects. The agency of insects such as dung-flies has been observed in nature, and also demonstrated experimentally.

Scatophaga stercoraria, the dung-fly, commonly occurs on Grouse moors. The eggs of the fly are laid in fæces, and hatch out there. The larvæ are large and somewhat active. They feed on the fæces of Grouse, which fæces may be infected with coccidian cysts. Dissection of such larvæ has shown the presence of oöcysts within their guts. When isolated larvæ were first well washed and then allowed to defæcate on a slide, the preparation of the fæces showed oöcysts when examined microscopically. Some of the pupæ also contained coccidian spores in their guts. The freshly hatched flies examined rarely showed spores, but as they proceed almost at once to ingest fæces, they rapidly become agents for distributing the spores. Dung-flies allowed to hatch out in the fæces of infected Grouse always contained coccidian oöcysts in their alimentary canal and fæces.

Laboratory experiments were made with the blow-fly, *Calliphora erythrocephala*. Eggs taken from the body of the parent fly were allowed to hatch out in fæces of an infected Grouse chick. The larvæ greedily ingested the cysts, which passed practically unaltered through their bodies. Some of the larvæ which pupated were washed very carefully and then dissected. They contained coccidian spores. Adults were fed on the infected material and oöcysts were voided in their excrement. The spreading of young flies, hatched infected, and of older ones that have fed on infected material, may aid, then, in the dispersal of Coccidiosis.

While experimental evidence of the action of *Scatophaga stercoraria* and *Calliphora erythrocephala* has been afforded in the laboratory, that is merely confirmatory of what may occur on some moors. Here on Scots firs, heather, and moss, numbers of flies are found, and dung-flies are known wherever Grouse droppings are to be found. The trail of birds can be tracked to some extent by the coprophagous flies, while lines of infection are produced by the birds as they pass down by small paths to their drinking places.

It may be of interest to note that houseflies (*Musca domestica*) have been shown experimentally to ingest coccidian oöcysts.

To summarise, wind and rain acting on infected fæces are probably the principal agents in dispersal, while the feeding habits of *Scatophaga* and other flies form subsidiary means of spreading the disease.

VII. DURATION OF VITALITY OF COCCIDIAN OÖCYSTS.

(α) *When the Oöcysts are kept in Water or very moist.*

Much moisture is present on many moors, and fæces of infected chicks contain coccidian spores which not only get washed into the soil, but also into tarns, etc., at which Grouse drink. It was, therefore, of some importance to determine the time required for the degeneration of the resistant spores of the parasite when in water.

Coccidian oöcysts with undifferentiated contents were placed in water, kept at about 20 degrees C. (July temperature), the water being replaced as required, to avoid evaporation effects. Ordinarily, the oöcysts develop sporocysts very rapidly—in two to three days. In the case of cysts kept in water, nine days elapsed before much change was noted. At the end of that period, a few oöcysts showed differentiated protoplasmic masses, and still fewer showed four sporocysts. Two days later many more oöcysts contained four sporocysts, and this progressive development continued for some days. Little signs of degeneration were seen until about the fortieth day, when some showed signs of gas bubbles in their interiors. Others, however, had completed their development, and their four sporocysts, apparently unharmed, were set free into the liquid. By the fiftieth day practically all oöcysts had either matured or degenerated, and the sporocysts had begun to degenerate.

From the above experiment, the conclusion is that the development of oöcysts and sporocysts is delayed by the presence of much moisture, but that the power of infection is retained for a long time by means of the sporocysts.

Very damp air has similar effects.

(β) *When Fæces are merely kept and allowed to dry on the outside.*

When freshly voided soft droppings of Grouse containing coccidian oöcysts are allowed to dry, the oöcysts in the surface layers rapidly develop sporocysts, the inner ones remaining unaffected.

Fæces kept *en masse* in covered dishes for as long as twelve months have

retained the power of infecting birds, as I have been able to show experimentally. Such material contains undifferentiated oöcysts still, while its outer layers mainly contain oöcysts with four sporocysts within them.

(γ) *Development under Different Conditions of Temperature.*

For experimental purposes, it was sometimes necessary to delay the development of sporocysts. This was easily done. The oöcysts in fæces were transferred to a chamber kept at 10 degrees C., having been previously kept at 15 degrees C. This change was sufficient to delay all further development for a considerable time. Smaller changes of temperature also arrested the development of sporocysts, though the effect naturally was not so marked.

Changes of temperature and moisture on the moors might result in the occurrence of occasional outbreaks of disease after the first attack had passed off. Moisture and coolness retard the development of certain oöcysts for a considerable time, during which period the disease disappears. A return of conditions favourable to the *Coccidium* then ensues, rapid development of sporocysts occurs, and a fresh outbreak of disease is initiated.¹

Unfortunately, it is difficult to follow the course of the disease under natural conditions on the moors; the greatest mortality occurs among very small chicks, and the dead bodies are rarely found. It might be possible for nearly every Grouse chick on a moor to die without the owner or his gamekeepers being aware of the fact. In such cases it is only when the stock is inspected in July and August that it is discovered that there is a scarcity of young birds, and various hypotheses are put forward to account for their mysterious disappearance (*vide* chapter ii. pp. 14-16). It is significant that one of the causes most commonly given is drought, *i.e.*, that a long period of hot, dry weather in May and June has caused the bird to die from want of water. We now know that young Grouse chicks seldom, if ever, die of thirst,² whereas we also know that dry heat is not unfavourable to the development of the oöcysts.

VIII. EFFECTS OF CERTAIN REAGENTS ON COCCIDIAN OÖCYSTS.

Certain experiments were made with a view to finding a means of destroying oöcysts without killing all other forms of life.

This is not an easy matter. While such strong reagents as caustic potash will slowly dissolve the oöcysts, their application is not practicable on Grouse moors.

¹ It is possible that the second outbreak of the disease will not be so fatal as the earlier one, owing to the increased age of the birds.

² *Vide* chap. iv. pp. 93-94.

Salt produces plasmolysis in the end; but the process is rather slow, and the salt is too readily dissolved in dew and rain, and so merely soaks into the soil.¹

Quicklime destroys the oöcysts and sporocysts. It also causes the fæces to cake, thereby preventing scattering of the spores. It is somewhat doubtful whether lime could be applied on a large scale. It might be somewhat harmful to the feet of the birds, apart from the difficulty of distributing it over large areas. Where the area of infection is small, it is probable that the application of lime to the soil would be of service. My experiments on a small plot of heather at Cambridge have shown that small quantities of lime dressing are not detrimental to heather.

Gas lime and *slaked lime* also are useful, but each is open to the same objection as quick lime. Lime in one form or another certainly seems to have the best and most rapid action on coccidian oöcysts of any reagent that I have tried.

Salicylates.—Salicylic acid and sodium salicylate act rather slowly on coccidian oöcysts when mixed with them. Both chemicals tend to deliquesce, and the fæces mixed with them remain fluid for a longer period than they otherwise would. The oöcysts become wrinkled and ultimately destroyed, but the contents take longer to degenerate than when lime is used.

Ferrous Sulphate.—Copperas or green vitriol is useful to some extent in destroying coccidian oöcysts, but like salicylates it is somewhat slow in action. A dusting of ferrous sulphate on the moors would probably be beneficial, for the combined iron present might be taken up in small quantities by Grouse and, by acting as a general tonic, might enable the birds to resist Coccidiosis the better if they became attacked. Ferrous sulphate in the proportion of 10 grains to the gallon of drinking-water has been found of service by the writer in the treatment of Coccidiosis in young fowls and young Pheasants. Some keepers and breeders, at my suggestion, have used *catechu* in the drinking-water with success.

Sodium Nitrate.—Nitrate of soda mixed with fæces destroyed the contents of the oöcysts after some time, but the length of time required for its effective application would militate against its use on a large scale.

In my experiments at Cambridge, three portions of infected fæces were mixed with equal quantities of lime, sodium salicylate, and ferrous sulphate respectively, and were kept in open dishes, exposed to the action of the weather. The results obtained may be shortly given.

In the case of *lime*, the fæces rapidly formed a caked mass. In a fortnight

¹ However, in this connection see Hammond Smith, *The Field*, August 20th, 1910. Suppl. p. viii.

the oöcysts were shrunken and wrinkled, and some showed cracks. At the end of three weeks, the cysts were more broken up and the contents largely disintegrating, while after a lapse of two months there was a difficulty in finding spores at all. Bacteria were not found after lime treatment, and there was only a slight fæcal odour noticed.

Sodium salicylate added to fæces rapidly deliquesced, in fact the mixture was quite liquid in less than three hours. After a fortnight's interval, the cysts appeared to be slightly shrunken, while fæcal odour was noticeable. A month later, the oöcysts were more shrunken and a few free sporocysts were found, while ten weeks after treatment, a slight smell was still perceptible, and the oöcysts present were shrunken and showed oily contents.

Ferrous sulphate (copperas) had much the same effect as sodium salicylate, but did not deliquesce. Though its action at first seemed to be rather less effective, it secured the same result ultimately.

IX. CONCLUDING REMARKS.

The ravages of Coccidiosis among Grouse chicks may be under-estimated on the moors, since the tiny corpses of the birds lie hidden among the heather.

While it is relatively easy to take preventive measures in the case of Coccidiosis in fowls, it is most difficult to take active measures in the case of Grouse. The remedy of heather burning is drastic, and coccidian spores, which are present in the tract burned, are then destroyed. However, heather is rather slow-growing, and so heather-burning, while efficacious, is somewhat restricted in its area of application. Lime dressing is destructive to spores of *Coccidia*, and could probably be utilised in the case of limited outbreaks of disease among Grouse chicks. The effect of lime on the growth of heather should first be carefully investigated on a large scale (*see* p. 265). Any condition tending to raise the general vitality of the birds also makes them much more resistant to disease. An abundant supply of healthy young heather, by raising the general standard of health of the birds, is probably one of the best safeguards against the insidious disease, Coccidiosis.

PART III.—COCCIDIOSIS IN GAME BIRDS AND POULTRY: SOME PREVENTIVE MEASURES, SUGGESTIONS, AND TREATMENT.

It may be of interest and importance to collect notes on various preventive measures which have come under my own practice and observation, more

especially since the preceding articles were written, and in addition to the measures therein mentioned. These preventive measures relate especially to fowls and pheasants, but should the hand-rearing of Grouse ever assume large proportions, then such measures may be applied directly thereto.

Recalling the old saw that “Prevention is better than cure,” I would first reiterate my former remarks:—

(1) All corpses of Grouse or Grouse chicks infected with Coccidiosis should be burned, not buried (*see pp. 251, 257*).

Burn infected corpses.

(2) Heather burning, as far as practicable, is efficacious in destroying coccidian cysts, worms’ eggs, etc., in the tract burned (*see p. 266*).

Heather-burning.

Regarding the first of these remarks I would point out that every buried diseased bird is a new source of infection, and the polluted soil is distributed in many and unseen ways by earthworms, the round worms of the soil, carnivorous beetles, moles, etc., so that the infection can be extended over a much wider area than was originally the case.

In regard to pheasantries in which havoc has been wrought by Coccidiosis, it is as well to consider the direction of the prevailing winds, and to place the new rearing pens in such a position that they are not wind-swept from the infected and fouled areas. This is not an easy matter in many instances, but should be observed wherever possible.

Consider direction of prevailing winds.

In the case of birds kept entirely or partially under domesticated conditions (*e.g.*, fowls, hand-reared pheasants, Grouse in captivity), great care should be taken to burn all droppings and to prevent fouling of food and drink as far as possible. This can be achieved to a considerable extent by providing removable boards on which food and drink can be placed, as has been suggested by Dr Hammond Smith. These feeding boards should be frequently cleansed and scrubbed. All food débris should be burned. The pens should be so constructed that easy cleansing can be done daily. Lime-washing of all coops, breeding-places, perches, etc., at least once a week is useful. Wherever possible healthy birds should be taken off the infected areas, and their coops, etc., placed in new positions, as remote as possible from the former ones. The fouled soil should then be thickly treated with quicklime, which, after an interval of about a week, should be well dug into the soil, the latter being turned to a depth of at least $1\frac{1}{2}$ feet. No birds should be raised on this land for at least a year. Where the infected run is relatively small, the

Burn all infected droppings.

Removable feeding boards.

Lime-washing pens.

Lime any fouled soil.

top soil can be taken off to a depth of 3 or 4 inches and then burned. Even under this condition it is advisable to lime the soil.

It is useless to remove *heavily* infected stock to fresh places, for it is far better to destroy such birds and to place healthy stock on fresh, unpolluted grounds. All other suspected birds should be isolated, and careful examination made of their excrement. In the case of epizootics among fowl-chicks one recent experience that I had was of a case where over fifty birds died in a very short time of undoubted Coccidiosis. Tracing the history of the remainder I found they had come from broods reared by handsome hens obtained from an estate where, on inquiry, I found that there had been heavy mortality from Coccidiosis during the previous year. The mothers and foster-mothers were all carefully isolated, and examination made of their fæces from day to day. In a very few days two fine hens were discovered whose dejecta showed daily crops of oöcysts of *Eimeria (Coccidium) avium*, and I do not think there is any doubt that these two birds had become chronics, and that their excrement had fouled the large grass run, and was the source of the trouble among the young birds. It may be added that washings of the grass and clover in the run also yielded the oöcysts of the parasite when examined microscopically.

The importance of considering the possible infection of foster-mothers in pheasant-rearing is already recognised.

Fowls and turkeys should never be reared on grounds where much mortality from "white diarrhœa" or "blackhead" has been known to occur. If the original occupants of the land were turkeys the oöcysts of *E. avium* producing "blackhead" are certain to be present in the soil, and when taken up with grit, food, or drink by fowls produce the Coccidiosis popularly known as "white diarrhœa," especially in young birds. Conversely, fowls can be the source of infection of turkeys. Pigeons feeding in infected fowl-yards themselves become infected, and whole cotes have been wiped out by Coccidiosis thus acquired.

Where poultry are kept in wired runs it is well to provide an overhead wire or net covering. Not only pigeons, but sparrows, visit poultry yards, etc., for food, and there take up coccidian cysts which, voided elsewhere in their droppings, serve as new sources of infection. The damage thus done by sparrows, in their wanderings and flights, as

Remove
healthy
stock.

Mothers or
foster-
mothers
may be
chronics,
and infect
young.

Fowls and
turkeys
may infect
each other.

Pigeons
and
sparrows
may spread
infection.

agents in the spread of disease can be easily inferred. The access of such birds to infected spots should be prevented as far as possible.

Should incubators be used for hatching chicks, these should be carefully disinfected a few days previous to their use, care being taken that no fumes are apparent when the eggs are introduced. The eggs themselves, whether for natural or artificial incubation, should be wiped with some disinfectant solution—90 to 95 parts of alcohol (or strong methylated spirit) with 10 or 5 parts of water respectively can be used for this purpose.

Eggs for incubation: wipe with alcohol.

Treatment.

As Coccidiosis is nearly always accompanied by anæmia, I have found that a little *ferrous sulphate* dissolved in the drinking water given to infected birds is of service (*see my remarks on p. 265*), its tonic action helping them to make a better resistance against the disease.

Ferrous sulphate in drinking water.

I have carried out direct treatment of Coccidiosis in the case of fowls, pigeons, hand-reared pheasants, and canaries, while Dr Hammond Smith has also tried the treatment that I had found successful in the above birds, on the hand-reared Grouse at Frimley, with satisfactory results. At two large poultry farms, where serious outbreaks of Coccidiosis occurred, the owners, at my suggestion, also tried the treatment detailed below, with, I am glad to say, uniform success. I have much pleasure in thanking Dr Annie Porter for help in some of these investigations.

When Coccidiosis was diagnosed early by cysts in the droppings, the infected birds were supplied with drinking water in which crude *catechu* was dissolved—10 to 15 grains of catechu being dissolved in a gallon of water. The solution so obtained was of a deep sherry or old ale colour. It should be noted that the catechu solution always darkens on keeping; but this does not affect its curative properties to any extent. The fowl chicks, pheasants, etc., were given this strength of solution for ten to fourteen days, and if the voiding of oöcysts had then entirely ceased for several days the dosing was discontinued. If, on the other hand, passage of oöcysts continued during the ten days of treatment, though steady decrease in their numbers occurred, the birds were then given water containing 5 to 8 grains of catechu per gallon for a further period, until practically no oöcysts were found in their fæces. Usually the first treatment, with the stronger dose, was sufficient. The birds showed no dislike of the catechu-water, but drank it readily.

Catechu in drinking water.

In very severe cases, treated late, as much as 20 grains of catechu per gallon of water have been administered; but as a rule this strength is too great, and the birds become constipated.

In my earliest experiments, ten fowl-chicks, aged fourteen days, infected with Coccidiosis, were all cured, while twelve pullets suffering from a mixed infection of Coccidiosis and worms were also satisfactorily treated. From experience gained with these cases I was able to help breeders with whom I was acquainted. Some of the results are as follows:—

At a large farm in Cambridgeshire, where some three hundred head of poultry are kept, an outbreak of Coccidiosis occurred. Catechu was given to all the birds in their drinking water, and after its administration no further deaths occurred, and the majority of the birds were perfectly well in ten days; nor was there a return of Coccidiosis. After treatment the birds were all removed to a fresh run.

At a Sussex general poultry farm where fowls, geese, ducks, turkeys, and pigeons are raised, and about two thousand head of birds are always present, catechu has been used now for some time in treating sudden outbreaks of Coccidiosis—usually after the introduction of new stock for breeding purposes. At the same farm a few pheasants are reared in captivity, and on one occasion a brood of six young pheasants (four weeks old) were in a very bad state owing to Coccidiosis; but all recovered after the administration of 10 grains of catechu per gallon of water for ten days.

Recently in an epizootic among fowls at Cambridge, in which some seventy fowls were given catechu at my suggestion, all recovered. But a curious reflex occurred, for an outbreak of Coccidiosis occurred among a number of pigeons that used to come to the poultry run for grain. As the pigeons in question were of some value, they, too, were confined in an aviary and treated with a 10 grains per gallon solution of catechu. Twenty recovered out of twenty-one treated, one bird being accidentally killed.

The latest case of Coccidiosis that I have encountered is that of two canaries belonging to a friend of mine. Five birds out of an aviary of seven had already died, and the others were very sickly when they were first brought to my notice. Catechu in a dose of 5 grains per gallon was given them. After a week the two treated birds showed no oöcysts in their fæces, and had recovered their song.

Some ailing Grouse, of varying ages, reared in captivity at Frimley, were given catechu in their drinking water. All showed marked improvement in a

short space of time. I have to thank Dr Hammond Smith for his help and enthusiasm in treating the birds.

Concluding Remarks.

While the successful combating of Avian Coccidiosis appears to lie in strict attention to cleanliness, and to the adoption of stringent preventive measures—such as I have indicated—yet, where the treatment of Coccidiosis is practicable I believe, from my experiments and the application of their results, that catechu has been proved to be of very definite service.

References to Literature.

- COBBETT, L., and GRAHAM-SMITH, G. S. (1910).—"An Investigation of the Pathology of 'Grouse Disease.'" Journ. Hygiene, x. pp. 1-36, 5 pls. (*Vide* chapter xii. p. 273.)
- DOFLEIN, F. (1909).—Lehrbuch der Protozoenkunde. 914 pp. G. Fischer, Jena. (Coccidia, pp. 616-653.)
- FANTHAM, H. B. (1909).—"Coccidiosis in Grouse Chicks" (Prelim. Note). Abstract of Proc. Zool. Soc. Lond., No. 76; also P. Z. S. 1909, pp. 886-887.
- FANTHAM, H. B. (1910).—"The Morphology and Life-History of *Eimeria (Coccidium) avium*: a Sporozoön causing a Fatal Disease among Young Grouse." Proc. Zool. Soc. Lond. 1910, pp. 672-691, 4 pls. (*Vide* chapter xi. p. 235.)
- FANTHAM, H. B. (1910).—"Experimental Studies on Avian Coccidiosis especially in relation to Young Grouse, Fowls, and Pigeons." Proc. Zool. Soc. Lond. 1910, pp. 708-722, 1 pl. (*Vide* chapter xi. p. 252.)
- HADLEY, P. B. (1909).—"Studies in Avian Coccidiosis. I. White Diarrhoea of Chicks. II. Roup of Fowls." Centralbl. f. Bakteriöl., Abt. i., Orig., 50, pp. 348-353.
- LABBÉ, A. (1896).—"Recherches zoologiques, cytologiques et biologiques sur les Coccidies." Arch. Zool. Expér. et Gén., ser. iii. t. 4, pp. 517-654, pls. 12-18.
- LABBÉ, A. (1899).—"Sporozoa" in Das Tierreich, Lief. 5, pp. 61, 68.
- M'FADYEAN, J. (1894).—"Some Observations regarding the *Coccidium oviforme*" and "Intestinal Psorospermiosis in the Pheasant." Journ. Comp. Path. & Therapeutics, vii. pp. 131-137.
- METZNER, R. (1903).—"Untersuchungen an *Coccidium cuniculi*." Arch. f. Protistenkunde, ii. pp. 13-72, pl. ii.
- MINCHIN, E. A. (1903).—"Sporozoa" in Lankester's "Treatise on Zoology," pt. i. fasc. 2. (*Coccidiidea*, pp. 204-238.)
- MORSE, G. B. (1908).—"White Diarrhoea of Chicks, with Notes on Coccidiosis in Birds." Circular 128, U.S. Dept. Agricult., Bureau of Animal Industry.
- NEUMANN, L. G., and MACQUEEN, J. (1905).—"A Treatise on Parasites and Parasitic Diseases of Domesticated Animals. 2nd edition, 697 pages. London: Ballière. (See pp. 404-417.)
- PERRONCITO, E. (1876).—"Nuove caso di psorospermiosi intestinale in una gallina." Annali Accad. Agricoltura, Torino, xix. i.
- PFEIFFER, R. (1892).—"Die Coccidienkrankheit der Kaninchen." Berlin.

- RAILLIET, A. (1895).—*Traité de Zoologie médicale et agricole*. 2nd Edition. 1303 pages. Paris: Asselin et Houzeau. (*See* pp. 142-144.)
- RAILLIET, A., et LUCET, A. (1891).—"Note sur quelques espèces de Coccidies encore peu étudiées." *Bull. Soc. Zool. France*, xvi. pp. 246-250.
- RETTGER, L. F. (1909).—"Further Studies on Fatal Septicæmia in Young Chickens, or 'White Diarrhoea.'" *Journ. Med. Research*, xxi. pp. 115-123.
- SCHAUDINN, F. (1900).—"Untersuchungen über den Generations-wechsel bei Coccidien." *Zool. Jahrbücher, Abt. f. Anat.*, xiii. 2, pp. 197-292, 4 pls.
- SILVESTRINI, A., e RIVOLTA, S. (1873).—"Psorospermi epizootica nei gallinacei." *Giorn. d anat. fisiol. e patol. de animali*, Pisa, v. pp. 42-53.
- SIMOND, P. L. (1897).—"L'évolution des Sporozoaires du genre *Coccidium*." *Ann. Inst. Pasteur*, xi. pp. 545-581, 2 pls.
- WASIELEWSKI, Th. von (1904).—"Studien und Mikrophotogramme zur Kenntnis der pathogenen Protozoen." Heft i., *Coccidia*. 118 pp., 7 pls. Leipzig: J. A. Barth.

CHAPTER XII

"GROUSE DISEASE"—CONTINUED—PATHOLOGY¹

By Dr L. Cobbett and Dr G. S. Graham-Smith

THE fact that wild animals are subject, like man, to diseases does not obtrude itself upon our notice, probably because they often hide themselves when ill, and creep into some corner to die, and perhaps because they have less aptitude for expressing their sufferings. However this may be, they bear so generally the aspect of perfect health that when attacked by a serious epizootic disorder, the latter gets dubbed with the name of the species it attacks; and so one hears of silk-worm disease, horse sickness, or swine fever, as though these were the only diseases from which those species suffer.

Introduc-
tion.

Disease in
wild
animals.

The Grouse, like other animals, suffers, doubtless, from a variety of diseases and disorders, but one of these, it is held, so far exceeds all the rest in importance that it has earned for itself the name of "Grouse Disease." Sportsmen and gamekeepers bear undivided testimony to the existence of this epizootic, which is observed with varying severity and regularity in spring and autumn; but it is not easy to be certain whether in "Grouse Disease" we have to do with a specific infectious disease, as is generally assumed, or merely with a series of disastrous consequences set in train by unusual privation, due perhaps to a bad season. Still less easy is it, in the case of any given bird, to tell whether or not it is suffering, or has suffered, from "Grouse Disease," especially at a time when birds are dying in unusual numbers; for even if we agree that there is a specific infection, we must admit also that privation claims its toll, and which of the two our bird is suffering from is not easy to decide, even after it is dead, for "Grouse Disease" has no characteristic symptoms, or very obvious macroscopic lesions.

Disease in
Grouse.

¹ Reprinted from *The Journal of Hygiene*, vol. x., No. 1, June 1910.

Our work has been done both with diseased and healthy birds. The former were caught by the keepers in a feeble or dying condition, at times when dead birds were being picked up in considerable numbers on the moor, and it was consequently believed that "Grouse Disease" was prevalent. But the mortality then was, we believe, not very great, in fact insignificant when compared with the really bad years such, for example, as 1873, and it is, we suppose, just possible that we never came across the genuine epizootic "Grouse Disease" at all.

The diseased birds which were subjected to bacteriological examination were nearly all caught alive and brought or sent to the temporary laboratory. Some, of course, died on the journey, but in only a few preliminary instances were cultures made from the latter, and then only when it was exactly known when the bird was last seen alive.

In addition to these birds from which cultures were made, many others which were picked up dead were examined for lesions and gross parasites. As will be easily understood the difficulty of obtaining diseased birds alive was very great, and the number fully investigated therefore very small.

The control observations on normal birds were more numerous; for, through the kindness of the members and correspondents of the Committee and others, we had no difficulty in obtaining as many as we wanted. Some few of these were examined in Scotland, but the great majority were received alive in our laboratory at Cambridge. A considerable number of these were caught for us by the keepers, and since it is no doubt easier to catch a feeble bird than a strong one, it may be that they do not fairly represent the average normal bird. It is probable, however, that they do not fall far short, if at all, of this standard, for they were plump and of good weight. They, of course, contained numerous entozoa, as do also the strongest birds which fall to the gun. The rest were hand-reared birds kept in captivity.

The first to attribute "Grouse Disease" to a living parasite was, we believe, Cobbold¹ (1873) who drew attention to the presence of the small nematode worm, *Trichostrongylus pergracilis*, often in large numbers in the cæca of Grouse which were supposed to have died of the disease. Nineteen years later Klein² (1892) investigated the disease, and came to the conclusion that it was "an acute infectious pneumonia" caused

¹ The "Grouse Disease," the *Field Office*, London, 1873.

² "The Etiology and Pathology of Grouse Disease, Fowl Enteritis and some other Diseases affecting Birds." London: Macmillan & Co., 1892.

by a specific bacillus, which he found in the blood and organs of birds which had succumbed to the disease. But neither of these theories of "Grouse Disease" has found general acceptance. Against Cobbold's view is often urged the well-established fact that *Trichostrongylus pergracilis* is present practically without exception in all normal wild Grouse (and often too in extraordinary numbers) and it has never hitherto been clearly shown to be more numerous in individuals believed to be suffering from "Grouse Disease" than in others. Klein's bacillus on the other hand has long been suspected of being no other than *Bacillus coli*, which, as is well known, rapidly invades the tissues after death. C. G. Seligmann, who was the first to investigate the bacteriology of "Grouse Disease" for the Committee, but who was unfortunately called away for other work before they were completed, had already, in 1907, come to the conclusion that Klein's bacillus was one of the *coli* group, and was not the cause of "Grouse Disease." To these points we must return when we have recorded our own observations.

It is necessary at this stage to explain how we came to be associated with the work, and what facilities we had for carrying it out.

"Grouse Disease" having been reported in Scotland early in May 1908, we were invited to undertake bacteriological investigations, and accordingly Dr Cobbett proceeded north to commence preliminary work. Some rooms at Beaufort Castle were converted by Lord Lovat into a temporary laboratory, and every effort made by his staff of keepers to procure diseased birds in a living condition. At the same time owners of Grouse moors in the neighbourhood were asked to procure living sickly birds if possible. Some days later a move was made to Mr Perrins' moor at Ardross, where Mr Cuthbert kindly placed a room in his own house at our disposal for use as a laboratory. The visit terminated after a week, but during the time eleven diseased birds and one normal bird were examined together with others picked up dead on the moors. The latter were, of course, useless for bacteriological examination since in all cultures made from the organs of birds which have been dead for some time, whether diseased or healthy, and of birds which have been shot and wounded in the abdomen, *Bacillus coli* and other intestinal bacteria occur in large numbers.

A second visit to Scotland was made from August 25th to September 1st. During that time eight fresh Grouse were examined for bacteria, one being a bird caught when obviously ill on Cawdor Moor and received alive.

After this, work was continued in Cambridge on normal birds which reached us alive, and on sickly birds caught alive, immediately killed and packed in ice and sent to us from time to time from various moors as occasion offered.¹

During the visits to Scotland it was, of course, not possible to carry out all the precautionary measures which are described later as having been taken when working in our own laboratories at Cambridge, but the most important of these precautions were observed, such, for example, as plucking the birds before they were brought into the laboratory, the free use of the flame for singeing, and of the actual cautery for destroying any stray particles of feather, and for burning the skin through which the incisions were made. In the preliminary experiments also the method of getting at the lungs from behind, which is described later, was adopted; and emulsions of the organs were made between sterilised plates; but the glass frame, in which this was done at Cambridge, had not been adopted at the time of the earlier experiments.

One of the first objects of the experiments was to seek for Klein's bacillus, and to compare it with other members of the colon group in the light of the great advances in bacteriology since Klein's observations were made eighteen years ago. The next was to look for characteristic lesions.

The preliminary observations in Scotland showed at once the presence of bacilli of the colon type, which could not be distinguished from Klein's bacillus, in the livers and sometimes in the other organs of diseased Grouse, but it soon became evident that these micro-organisms might be present also in the organs of Grouse presumably quite healthy. No pneumonia was seen in any of the birds examined by us in a perfectly fresh condition, the lungs being always pale pink in colour and free from congestion. In birds picked up dead on the moor it was not always easy to make a definite statement about the lungs as they were often deeply stained and otherwise altered, but in the fresher specimens it was apparent that there was no pneumonia. In the fresh, diseased birds the livers were not obviously altered, though in those birds which were picked up dead they often showed more or less of that blackish colour, which has sometimes been described as characteristic of "Grouse Disease," but which is certainly due to

¹ Cultures were never made except from birds which reached us alive.

post-mortem changes. We had the opportunity of seeing many of these birds, for Dr E. A. Wilson, the Committee's field observer, was working at Beaufort at the same time as ourselves, and it was he who first showed to us the entozoal and other parasites of the Grouse. He, too, it was who first pointed out to us that the most notable lesions were in the cæca. The mucous membrane often appeared deeply reddened along the convexities of the longitudinal ridges, and sometimes thickened. To the naked eye, or with the aid of a hand lens, it was plain that considerable pathological change had taken place here, but there was no obvious ulceration. There were always large numbers of *Strongyli* in these cæca. This condition was most advanced in birds which were picked up dead, but it was no *post-mortem* change, for it was found also in weakly birds which were brought to us alive. There were in these birds also many large tapeworms, *Davainea urogalli*, in the intestine, fragments of which were found, though rarely, in the cæca also. In the birds examined during the spring there were invariably enormous numbers of the slender tapeworm, *Hymenolepis microps*, in the duodenum, and the mucous membrane of this part of the intestine was reddened.

It was therefore necessary to carefully compare normal and diseased birds (a) as to numbers of *Strongyli*; (b) as to liability to contain living bacilli in their organs; (c) to make a detailed examination of the lesions in the cæcal mucous membrane, and to see what relation this had to the nematodes on the one hand, and the bacilli on the other; and lastly (d) to find out whether or not, the bacilli exerted any pathogenic action. It seemed possible that the *Strongyli* might be the cause of the changes in the cæcal mucous membrane; that these changes might admit the intestinal bacteria to the liver and other organs of the body, and that these together with other pathogenic products abnormally absorbed from the diseased cæca, or possibly the mere interference with absorption caused by that disease, might lead to the death of the birds.

All the diseased birds examined were considerably under weight and wasted. We never came across any instance of a bird dying plump and in good condition, unless indeed its death could clearly be attributed to some other cause, such as accident.

It was recognised from the first that, if micro-organisms were present in the organs in small numbers only, somewhat large amounts of tissue might

Presence of
entozoal
and other
parasites.

No diseased
birds found
in good
condition.

have to be used in order to obtain colonies on solid culture media. It was further recognised that the tissue would have to be crushed into a pulp, which could be spread more or less evenly over the surface of the medium, in order that any micro-organisms which might be present should have a chance of coming into contact with it.

Moreover, it was clearly seen that in carrying out experiments of this kind the chances of accidental contamination were not inconsiderable. The methods which were first employed in Scotland were later somewhat modified when the investigations were subsequently continued in Cambridge.

The precise conditions under which these experiments were conducted are matters of considerable importance, since upon them depend the reliability of the results which were obtained. We have therefore no hesitation in describing the methods in detail.

Previous to beginning an experiment the room was carefully prepared. All dust was removed from the window ledges and elsewhere, and the floor and bench were flooded with a mixture of glycerine and lysol to lay the dust. All the windows and ventilation shafts were closed during the actual operation of making the cultures. As a further precaution against aerial contamination the tissues were crushed inside a glass frame which was constructed as follows (Pl. XXXIX., Fig. 1):—Two sheets of plate glass, 21×8 inches, formed the top and bottom respectively, the former being supported on blocks of wood, which formed the sides. The back also was formed of a sheet of plate glass, and the front was closed by a curtain of linen, soaked in lysol, which could be partially turned back when required. The joints of the frame were made draught-proof by means of rubber tubing. On the floor of the frame another sheet of plate glass, which extended the whole length, but was 3 inches narrower than the bottom, was placed towards the back, so as to form a ledge near the centre of the floor, upon which the plates used for crushing the tissues could be conveniently manipulated, and yet be covered by the roof. The height of the frame from the top to this ledge was 3½ inches.

Before use the frame was washed out with a mixture of glycerine and lysol. In order to estimate the risk of aerial contamination agar plates were exposed on the bench and inside the frame during the whole period of time the cultures were being made.

The birds, if living, were killed by decapitation, weighed and immediately

Methods of making cultures from the organs of birds.

Precautions against aerial contamination.

PLATE XXXIX.

(1) APPARATUS FOR MAKING CULTURES. (2) ALIMENTARY CANAL OF GROUSE.

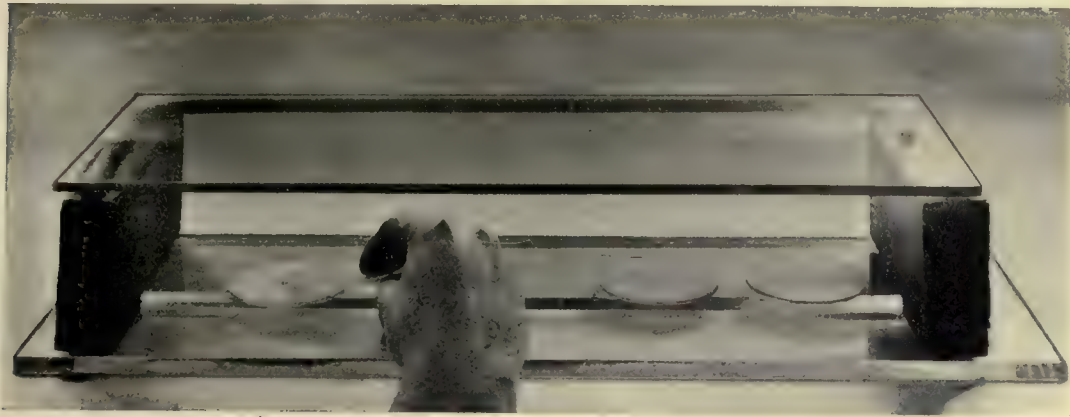


FIG. 1.

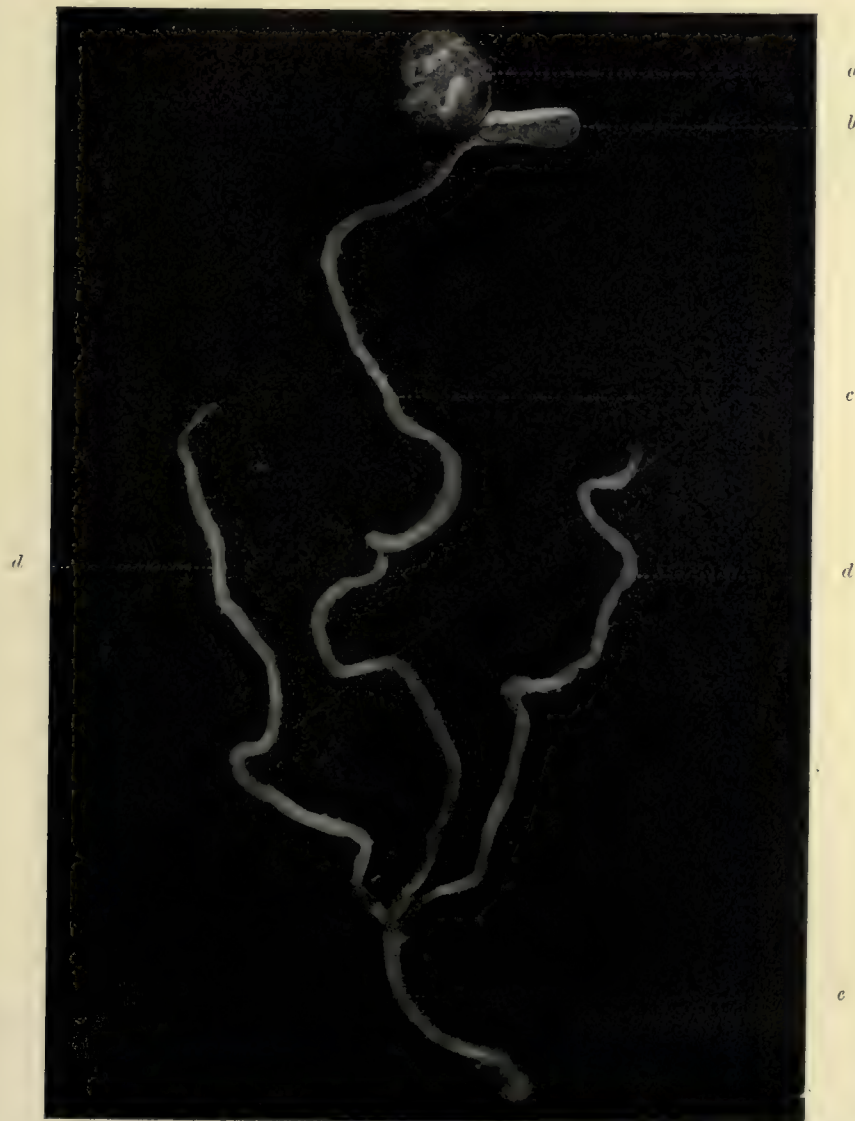


FIG. 2.

FIG. 1. ($\frac{1}{2}$ nat. size) showing the glass frame in which the crushing of the tissues was done. On the ledge are three pairs of ground glass plates. One of the plates of the pair on the left is being held up in the manner in which this was done preparatory to placing a piece of tissue between the plates.

FIG. 2. ($\frac{1}{3}$ nat. size) showing the alimentary canal of a normal Grouse (No. 81) from the gizzard to the anus. Gizzard (*a*), duodenum, enclosing the pancreas (*b*), intestine (*c*, *d*), and rectum (*e*).

plucked in an adjoining room. As far as possible all the feathers, except the larger ones of the wings, were removed, and the cloaca, if gaping, was plugged with a pledget of cotton wool. The smallest feathers appeared to us to be a particularly dangerous source of contamination, since some might be soiled with fæcal matter. Owing to their extreme lightness some of these, unless carefully destroyed, might float in the air and alight on to the tissues during the manipulations without being noticed. In order to obviate all chance of contamination from feathers the body of the bird after plucking was held in the flame until all the minute feathers had been completely destroyed.

Preparation of the bird.

A plumber's soldering iron, heated to redness, was freely used to burn the skin through which the incisions for removing pieces of tissue were to be made. The necessary incisions were then made without delay with instruments sterilised by boiling for at least half an hour. A fresh pair of scissors and forceps were used for removing the piece of tissue actually used for cultivation. Cultivations were made from each organ in turn, observing the precautions which have just been described in each case.

Method of obtaining portions of the organs.

Lungs.—The lungs were approached from the back. After the skin had been thoroughly seared with the iron the muscles under the scapula were transfixed with a knife and the scapula freed by carrying the knife out at its apex; the bone was then turned up and broken. Next two or more ribs were cut through with scissors, each in two places about half an inch apart, and a piece of the lung approximately equal in bulk to a cube one-quarter of an inch in all dimensions was cut out, and quickly transferred to the ground glass plates for disintegration.

Lungs.

Kidneys.—As the kidneys were approached from the back they were taken immediately after the lungs. A piece of the thin iliac bone, where it bulges outwards, was removed, care being taken not to force the intestines upwards during the process by pressure on the under side of the body. The satisfactory removal of portions of the kidneys was often a difficult matter, partly owing to the limited size of the opening which could be conveniently made in the bone, and partly owing to the nerve trunks which traverse the organs and render the extraction of portions difficult. In a few cases the intestine was wounded, but when this accident was perceived the attempt to obtain any further cultures from this bird was abandoned.

Kidneys.

Liver, Pancreas, and Spleen.—These organs were approached from the front by turning back the sternum after cauterising the whole ventral surface, and especially the lines of the incision. Culture tubes were sown from the liver always, but the pancreas was examined culturally on a few occasions only, and cultures from the spleen were not made when the organ was required for histological purposes. In the Grouse the spleen is extremely small, so that even when cultures were made the amount of material employed was considerably less than in the case of other organs.

Blood and Bile.—Samples of blood were obtained by plunging sterile pipettes through the heart wall after cauterisation. Bile was also obtained in glass pipettes from the gall-bladder, but the surface of the latter organ was not cauterised.

From each organ a piece, at least a quarter of an inch square, was removed by the methods just described, and placed on the surface of a ground glass plate. The plates used were 3 to 4 inches in diameter, and were ground on one side; these were sterilised by boiling and dried separately in the flame. As soon as they were dry the plates were placed in pairs, with their ground surfaces in contact on the glass ledge which has been described in the glass frame; in this situation they cooled rapidly. When a portion of an organ was ready to be ground up the upper plate of a pair was taken up and held in the fingers in such a way that about one-quarter of it overlapped an equal area of the lower plate. The piece of tissue was then placed between the overlapping areas and crushed. It was not found necessary to use powdered glass or other material to assist disintegration, because the organs of the bird, protected as they are from violence by the comparatively rigid skeleton, are much softer than those of mammals, and are easily reduced to the condition of an emulsion.

Before starting an experiment a series of sloped agar tubes were labelled two or three for each organ, and arranged on the bench in the order in which the organs were to be dealt with. As soon as a portion of an organ had been reduced to a pulp, a considerable quantity of the latter was taken up on a sterile platinum wire (bent into a series of loops so as to form a spatula), and spread over the surface of one of the agar tubes. The whole of the material crushed was left on the two tubes. In this way any living organisms that might be present had an

opportunity of producing colonies on the surface of the medium. In the case of nine birds (Nos. 20-28) anaerobic cultures were also made in Buchner tubes from all the organs, but as they did not yield anything more than the ordinary cultures, such cultures were not made in the later experiments. Control agar plates were exposed on the bench, and in the glass frame, during the whole of these manipulations.

The cultures were incubated at 37° C. and examined daily on the first few days, and subsequently at various intervals up to a fortnight. Colonies of *Bacillus coli* or *Streptococci* seldom appeared after twenty-four to forty-eight hours' cultivation, except when they grew out of one of the larger masses of tissue on the surface of the tube. The principal result of allowing the cultures to incubate for longer periods was to reveal the presence of moulds and streptothrices, and occasional spore-bearing bacilli and cocci in cultures from the lungs.

Examination of cultures.

The examination of the agar plates, exposed on the bench and within the glass frame during the progress of the experiments, showed that in spite of the long exposure very few colonies grew on them. *Bacillus coli* was never found, and moulds and streptothrices were uncommon. The commonest organisms were *Sarcina lutea* and cocci.

All organisms resembling *Bacillus coli* were isolated in pure culture, and the characters of their growth on agar, gelatine, and potato investigated, together with their staining reactions and motility. They were also cultivated up to fourteen days in milk, and in peptone water tubes containing glucose, lactose, mannite, saccharose, and dulcitate.

Identification of the organisms found.

Altogether thirty-five lactose fermenting organisms of the colon group were isolated from the organs of the birds and thoroughly investigated. All these organisms had the following characters in common:—Short, gram negative, non-spore-bearing bacilli with rounded ends. Greyish-white colonies on agar, gelatine never liquefied. Moist white or cream coloured growth on potato. Permanent acidity and clotting in milk. Most of them produced indol, and the majority showed some motility, especially in peptone water cultures.

Following MacConkey's¹ (1905) classification of the lactose fermenting

¹ A. MacConkey (1905). "Lactose-fermenting bacteria in Fæces," *Journ. of Hygiene*, v. p. 333.

bacilli, these organisms may be divided, according to their reactions, which are given in the following table, into four groups.

Group.	Type.	Glucose.	Lactose.	Saccharose.	Dulcite.	Mannite.	Milk.	Indol.
I.	<i>B. acidi lactici</i> (Hüppe)	A+G	A+G	0	0	A+G	A+C	+
II.	<i>B. coli communis</i> (Escherich)	A+G	A+G	0	A+G	A+G	A+C	+
III.	<i>B. coli communior</i> (Durham)	A+G	A+G	A+G	A+G	A+G	A+C	+
IV.	<i>B. lactis aerogenes</i> (Escherich)	A+G	A+G	A+G	0	A+G	A+C	+

0=No change.
A+C=Acid and clot.

A+G=Acid and gas produced.
+=Positive reaction.

Twelve organisms, namely those isolated from the livers of Grouse 3, 4, 7, 12, 44, 50, 56 and 60, from the lungs of 15, 50, and 57, and from the blood of Grouse 15, belonged to Group I.; three, isolated from the livers of Grouse 11 and 53 and from the lungs of Grouse 1, belonged to Group II.; eleven, isolated from the livers of Grouse 1, 6, 13, 16, 46, 51, 54, 58, 59, and 61, and from the lungs of Grouse 13, belonged to Group III.; and nine isolated from the livers of Grouse 2, 22, 23, 57, and 62, from the lungs of Grouse 22 and 56, and from the spleen and kidney of Grouse 22, belonged to Group IV.

Organisms belonging to all four groups were cultivated also from the caecal contents on various occasions.

An organism with the same general morphological and cultural characters, but differing in its fermentation reactions, was cultivated from the liver and spleen of Grouse 47, and from both lungs, spleen, pancreas and both kidneys of Grouse 51. This organism produces acid and gas in media containing glucose, mannite and dulcite, and acidity followed by alkalinity in milk. In media containing lactose and saccharose no change is produced. It corresponds therefore in its cultural characters with the *Bacillus enteritidis* (Gærtner) group.

Many of the other organisms found were similarly investigated, except moulds, streptothrices, cocci and spore-bearing bacilli; but in view of their extreme rarity it seems scarcely necessary to give their cultural characters in detail.

At an early stage in the investigations it began to appear probable that the presence of *Bacillus coli* in the liver and other organs of the Grouse was

related in some way to the numbers of *Trichostrongylus pergracilis* in the caeca. Up to December 1908 the Strongyli were only roughly estimated, but at that time a method of isolating and counting

them was devised and found to be practicable, and from that time onwards the Strongyli were counted in every case. The method was as follows:—The caeca were laid out straight on a board and opened throughout

The
method of
counting
Strongyli in
the caeca.

PLATE XL.

TEST TUBES CONTAINING *TRICHOSTRONGYLI PERGRACILIS*.

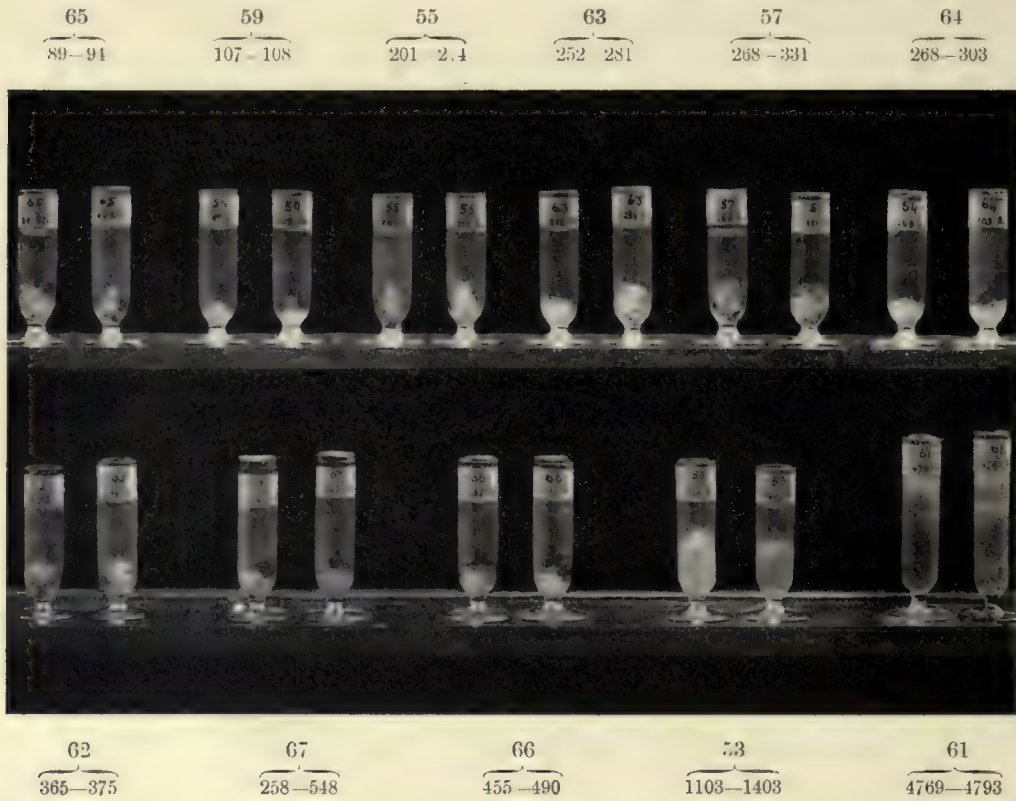


FIG. 3.

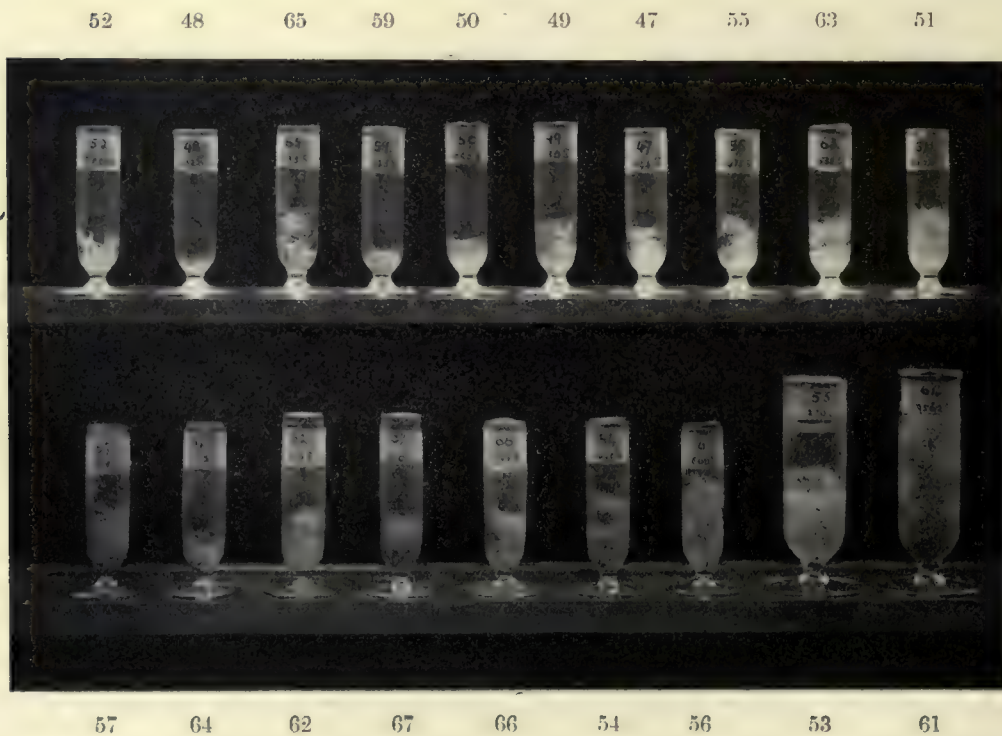


FIG. 4.

FIG. 3. ($\frac{1}{2}$ nat. size) showing small test tubes arranged in pairs containing the Strongyli collected from the two caeca of eleven Grouse. The serial number of the Grouse is written on the top, with the number of Strongyli present in each tube immediately below.

FIG. 4. ($\frac{1}{2}$ nat. size) showing small test tubes containing the Strongyli collected from both caeca of eighteen Grouse. No Strongyli were found in the caeca of Grouse No. 52, and in this case the test tube contains thirty-two specimens of *Heterakis papillosa*. The serial number of the Grouse is printed opposite each tube.

their length, their contents turned out, and their mucous membrane scraped. All the material liable to contain Strongyli was thus collected. Small quantities were shaken up with water in a large test-tube, and poured out little by little into a Petri dish containing water. With suitable illumination the Strongyli could be clearly seen and picked out with a mounted needle and counted. When the contents of the cæca were drier than usual, and did not readily break up when shaken with water, they were disintegrated by rubbing between the flat surface of a rubber bung and the bottom of a Petri dish. There can be no doubt that, while some Strongyli must have escaped notice, this method gave a close approximation to the numbers which were actually present—quite close enough for the purposes of our Inquiry. In nearly all cases the worms in the two cæca were separately counted, usually by different observers. As may be seen, by reference to Table I. and Pl. XL., Fig. 3, in all but two birds (Nos. 57 and 67) approximately equal numbers were present in the two cæca. We thought, therefore, that in our future investigations a sufficiently accurate estimation of the number of Strongyli might be arrived at by counting those present in one cæcum and doubling the number found.

TABLE I.—SHOWING THE RESULTS OF COUNTING THE STRONGYLI IN THE TWO CÆCA SEPARATELY.

Grouse No.	Strongyli.		Total.	
	One cæcum.	Other cæcum.		
52	0	0	0	23 specimens of <i>Heterakis papillosa</i> found in one cæcum and 10 in the other.
81	0	0	0	
58	54	59	113	
65	89	94	183	
59	108	127	235	1 specimen of <i>H. papillosa</i> in each cæcum.
46	131	128	259	
55	201	214	415	
63	281	252	533	
64	268	303	571	
57	331	268	599	
62	365	375	730	
67	285	548	833	
68	420	457	877	
66	455	490	945	
56	754	1114	1868	1 specimen of <i>H. papillosa</i> in each cæcum.
53	1103	1403	2506	
60	3118	2877	5995	
61	4769	4793	9562	

In the lungs, moulds and streptothrices were almost constantly found. The fact that they were absent in all but a very few of the tubes sown from other organs indicates that they were really in the birds' lungs during life, and did not get into the tubes as a result of contamination. Further, these results have been confirmed by observations on a number of other animals, both mammals and birds.

General
results of
bacterio-
logical ex-
aminations
of the
organs.

The other organs and blood were in the immense majority of cases free from cultivatable micro-organisms, except when *Bacillus coli* was present. Occasionally a single colony of some microbe would appear, perhaps a spore-bearing bacillus like *Bacillus subtilis*, or *Sarcina lutea*, or rarely a mould. On several occasions diphtheroid segmented bacilli were found. That these were sometimes accidental contaminations seems very probable, and in any case their numbers were so few as to be of little practical importance. Nevertheless, it may be that some were really in the living tissues during life, and this seems more probable in the case of the segmented bacilli, for these were sometimes found in cultures from the blood, which are less liable to contamination than those from the solid organs, as well as elsewhere. Moreover in one case (Grouse 37) they were also cultivated from the contents of the intestinal canal, but were only rarely met with on the exposed agar plates.

The whole question of the presence of bacteria in the living organs is in course of investigation by us, and we need not dwell further on the matter here, except in so far as *Bacillus coli* is concerned.

Beyond the œsophagus, crop, and gizzard the alimentary canal consists of the duodenum, intestine, paired cæca, and rectum (Pl. xxxix., Fig. 2).

The duodenum, a thin-walled light-coloured tube, 4 to 7 inches long, on which the vessels are clearly seen, forms a U-shaped loop of which the limbs lie in close contact with one another, the angular space on the ventral side being occupied by the pancreas. Next follows the intestine, a thicker walled tube of grey colour some 20 to 34 inches in length, and half an inch in diameter. From the junction of the intestine and rectum arise the paired cæca. Each cæcum consists of a short narrow portion with small lumen next the intestine, and a long wider portion between 1 and 2 feet, or even more, in length, and about one-third of an inch in diameter. At its distal end it tapers rather suddenly to a point

The ali-
mentary
canal of
the normal
Grouse.¹

¹ The measurements of the various parts of the alimentary canal vary greatly in different birds.

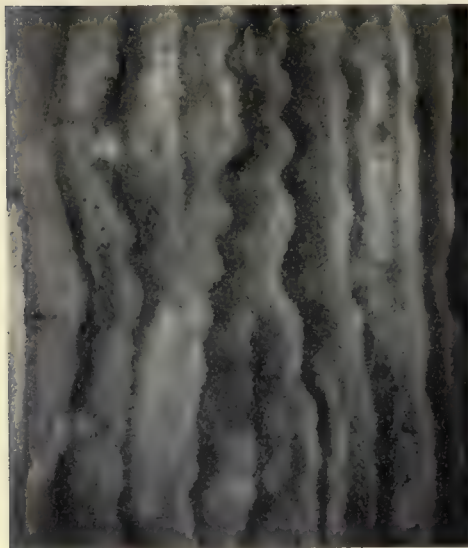
SECTIONS OF CÆCUM SHOWING *TRICHOSTRONGYLUS PERGRACILIS*.

FIG. 5.

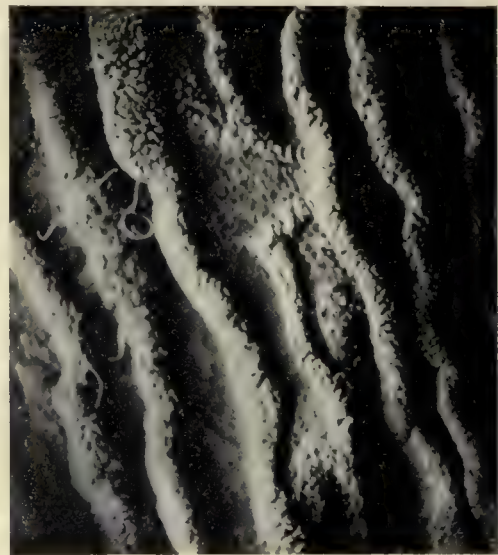


FIG. 6.

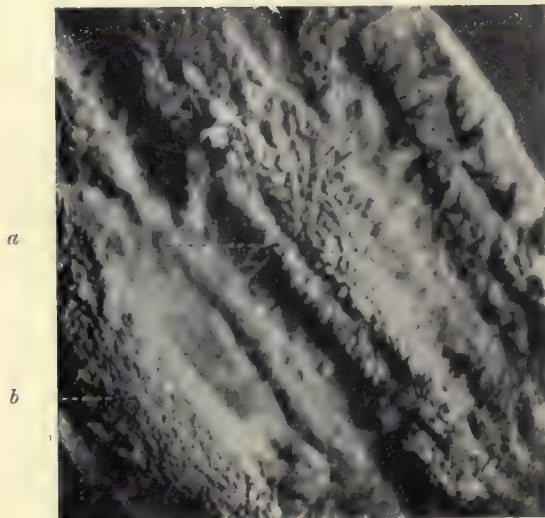


FIG. 7.



FIG. 8.



FIG. 9.



FIG. 10.

- FIG. 5. ($\times 5$) showing the internal surface of the cæcum of a normal Grouse (No. 81) after gentle washing. Several ridges are seen, some of which die away near the centre of the specimen. The whole surface is covered with small villi.
- FIG. 6. ($\times 5$) showing the internal surface of the cæcum of an apparently healthy wild Grouse (No. 69) after gentle washing. The ridges are greatly developed, and the villi larger and more prominent than in the preceding figure. A few worms can be seen.
- FIG. 7. ($\times 5$) showing the internal surface of the cæcum of a diseased Grouse (No. 73) after gentle washing. The ridges are very broad, and the villi in some places hypertrophied (a). In one situation the villi are so matted together that they are almost indistinguishable (b). At this spot a mass of dry material adhered to the ridge.
- FIG. 8. ($\times 5$) showing the internal surface of the cæcum of a diseased Grouse (No. 12) after gentle washing. The ridges are very prominent, but the villi are matted together to such a degree with cementing material that they are almost indistinguishable. Some of the ridges are united with the same material (a, b).
- FIG. 9. ($\times 100$) showing two specimens of *T. pergracilis* in section in the epithelium covering a villus.
- FIG. 10. ($\times 100$) showing a specimen of *T. pergracilis* in section surrounded by a ring of fibrous tissue.

Its walls are thinner than those of the intestine, and are marked by about nine longitudinal whitish lines. On opening the cæcum well-marked longitudinal ridges are seen, corresponding to the lines just described. Each ridge shows alternate thicker and thinner portions. Occasionally one of the ridges may be seen to die away or fuse with its neighbour. They occur throughout the whole length of the cæcum.¹

On examination under a Zeiss binocular microscope ($\times 8-33$) the mucous membrane of a Grouse (*e.g.*, No. 81) in which no *Strongyli* are present, after gentle washing in a stream of water, is seen to be regularly beset with small villi of uniform size, arranged closely together on the ridges, but more widely separated in the depressions, where they seem to be less well developed. They often appear club-shaped, more especially on the ridges, where their flattened terminations, lying closely together at a uniform level, give the surface a somewhat smooth and tessellated appearance (Pl. XLI., Fig. 5). In birds caught on the moor (*e.g.*, No. 69), apparently normal but infected with *Strongyli*, both the ridges and the villi are much larger (Pl. XLI., Fig. 6).

The rectum is a thick walled tube of greyish white colour, about 4 inches in length.

The contents of the gut vary much in different parts. The duodenum usually contains nothing but a white, slimy mucus. The intestine contains coarsely divided particles of food, and occasional grits from the gizzard. The contents of the cæca present a marked contrast to those of the intestine, consisting of a brownish or greenish pasty mass of finely divided material. The rectum contains usually only the coarser particles of food which have never passed into the cæca.

Duodenum. — At certain seasons of the year the duodenum of every wild bird examined was packed with the long thin tapeworm *Hymenolepis microps*. They were particularly numerous from March to May, and towards the end of August. Under these circumstances the contents appear to consist wholly of tenacious mucus, until shaken up in alcohol, when the worm becomes visible for the first time. No obvious pathological changes, except some reddening, were seen. *Trichosoma longicolle* was occasionally found in small numbers.

Pathological changes in the alimentary canal.

Duodenum.

Intestine. — The lower half of the intestine was often found distended with tangled masses of the large tapeworm, *Davainea urogalli*; they bear a less definite relation to season than does *Hymenolepis*. Portions

¹ For a fuller description of the alimentary canal of the Grouse reference may be made to chap. v. pp. 100 *et seq.*

of these worms are sometimes found bile stained. No pathological changes were noticed.

Cæca.—The appearance of the cæcum as seen from without varied; in some cases there were no obvious changes; in others the cæca appeared to be somewhat dilated, and sometimes they were mottled with lighter coloured patches. The contents, the main portion of which was semi-fluid, often contained—especially near the proximal ends—dry masses, which were very adherent to the mucous membrane, and which corresponded to the whitish patches seen from the exterior. Whenever one of these masses was peeled off numerous Strongyli could be seen stretched between the mass and the mucous membrane, obviously adherent to both. The dry attached condition of these masses strongly suggested that they consisted of material which had long been retained in the gut.

The small nematode, *Trichostrongylus pergracilis*, was often present in enormous numbers, occasionally amounting to thousands. They were particularly numerous towards the proximal ends of the cæca, especially in the dry masses just described. Except in one instance we never failed to find Strongyli in wild Grouse, and they were always present in large numbers in birds suffering from "Grouse Disease." The numbers present in wild Grouse did not appear to depend in any way upon the time of year. Portions of *Davainea* were on rare occasions seen in the cæca.¹

*Tricho-
strongylus*
nearly
always
present.

After washing in a gentle stream of water the mucous membrane frequently appeared reddened, especially in birds which were picked up dead on the moor. The reddening was present in many, but not in all, of the birds badly infested with Strongyli which were examined in a perfectly fresh condition. It was thought that this might possibly have been a *post-mortem* change, and some normal birds were kept after death for a few days before examination to see if the redness would appear in them; but it was not seen. When examined under a Zeiss binocular microscope ($\times 8-33$) the ridges were found to be thickened, especially in patches to which the dry masses already referred to were found adherent (Pl. XL, Fig. 7). The villi were very irregular in all situations, being in places greatly hypertrophied and club-shaped both in the depressions and on the ridges, and in other places atrophied, particularly on the thickenings just mentioned. In many cases the villi on the ridges were

¹ Pl. XLIV. shows in diagrammatic form the alimentary canal of the Grouse and the habitats of the more important intestinal parasites.

TRICHOSTRONGYLUS PERGRACILIS AND *DAVAINEA UROGALLI*.

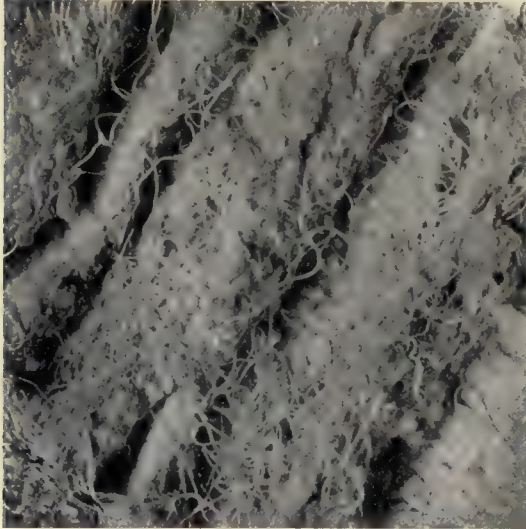


FIG. 11.

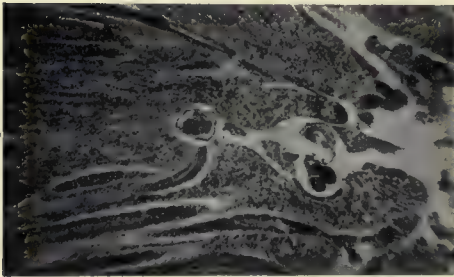


FIG. 12.



FIG. 13.



FIG. 14.

- FIG. 11. ($\times 5$) showing large numbers of *T. pergracilis* on the internal surface of the caecum of a diseased Grouse (No. 13).
 FIG. 12. ($\times 100$) showing a specimen of *T. pergracilis* (in section) between two villi. The epithelium has been lost and fibrous tissue (a) has been formed within one of the villi in the neighbourhood of the worm.
 FIG. 13. ($\frac{2}{3}$ nat. size) showing two tubes containing the specimens of *Davainea urogalli* (on the left) and of *Hymenolepis microps* (on the right) obtained from Grouse No. 11.
 FIG. 14. (nat. size) showing a tangled mass of *Davainea urogalli* (partially opened out) from the intestine of a Grouse.

embedded in some cementing material, which in microscopic sections appeared to be composed of a mixture of mucous and granular *débris*, which could not be removed by gentle washing. Even after free washing numerous *Strongyli* could be seen adherent to the mucous membrane, and frequently penetrating between the villi (Pl. XLII., Fig. 11). In some of the worst cases the ridges are so deformed as to resemble masses of coral, with smooth but irregular surfaces, on which the individual villi are frequently indistinguishable, and with cave-like depressions between them from which one or more *Strongyli* can be seen protruding (Pl. XLI., Fig. 8). These appearances, we believe, are due to the matting together of the villi and sometimes of the neighbouring ridges by the cementing material described above.

With the small amount of material at our disposal¹ it was impossible to follow out in detail the various changes which occur in the *cæca*, and we therefore confine ourselves to comparing the condition found in severely affected birds with that found in normal birds. In the investigation of the histological changes we had the advantage of the expert opinion of Mr T. S. P. Strangeways, Huddersfield Lecturer in Special Pathology, Cambridge.

Sections of the *cæcum* of the normal bird (No. 81) without *Strongyli* show the following structures.

There is under the peritoneum a well-marked muscular coat, and within this delicate areolar tissue supporting a layer of well-formed connective tissue on which the mucous membrane rests. At intervals the connective tissue layer projects towards the lumen of the gut forming the central core of the ridges which have been described. At their bases these prolongations appear bifurcated, and the spaces between the bifurcations are filled with fat and some large blood-vessels. Both the ridges and the depressions between them are covered with villi of fairly uniform length, which consist of a central core of vessels surrounded by a small quantity of delicate sub-epithelial connective tissue, together with a few lymphoid cells, covered with a single layer of columnar epithelium. Here and there in the depressions may be seen sections of lymphoid follicles covered with villi. The contents lying in the lumen of the gut consist of a mass of granular material and mucus (Pl. XLIII., Figs. 15 and 16).

Histological changes in the *cæca*.

Normal *cæcum* described.

Where no worms present.

Sections of the *cæcum* of an apparently healthy Grouse (No. 69), with many

¹ In twenty-six specimens the contents of both *cæca* were used for counting the *Strongyli*; and fourteen specimens arrived dead and therefore useless for minute histological examination.

Strongyli (1460), caught on the moor differ in certain respects (Pl. XLIII., Fig. 17). The muscular walls contain distinct bands of wavy, fibrous tissue. The quantity of fibrous tissue in the cores of the ridges seems to be increased; but fat is still present in the bifurcations. The ridges are large, and the villi are markedly increased in size, especially those situated near the free margins of the ridges. In the latter wavy bands of fibrous tissue may be seen; and lymphoid cells are found in considerable numbers within all the villi. The epithelium appears hypertrophied, but is not markedly irregular except over the villi on the free margins of the ridges. Worms are uncommon except in certain situations in the depressions, where they seem to be entangled in what appears to be dry, concentrated gut contents. No lymphoid follicles can be seen.

In a diseased Grouse (No. 6), in which the macroscopic changes are well marked, the following condition is found. The muscular wall contains well-marked strands of fibrous tissue. The fat at the bases of the ridges has completely disappeared, and the vessels show considerable thickening of their walls. The connective tissue in the cores of the ridges is also greatly increased in amount and in density, and the vessels dilated. The sub-epithelial connective tissue of the villi is also increased in amount, and the vessels in it dilated, and probably increased in number, and in some cases full of blood. The connective tissue is in most places loose and contains large numbers of cells, probably inflammatory in origin, and in some places, especially near the free ends of the villi and in the neighbourhood of the worms, shows fibroid change. The epithelium is proliferated and thrown into folds (Pl. XLIII., Fig. 18).

In a Grouse (No. 15) badly infected with Strongyli, and showing well-marked macroscopic lesions, all the changes just described are more evident. Much fibrous tissue is present in the muscular coat, and the walls of the vessels are very markedly thickened. The villi appear increased in size, and their connective tissue is more dense, and contains a considerable amount of fibrous tissue, replacing the more delicate connective tissue. In this tissue a large number of the nuclei are clearly those of newly-formed fibrous tissue, being elongated and spindle-shaped, though round cells are still present in considerable numbers. Nuclei of the former type are now found in all situations, and are not limited to the cores of the ridges as in the case of specimens from normal birds. The epithelium shows great proliferative changes, and is thrown into irregular folds. In all specimens from diseased birds the lymphoid follicles are indistinguishable (Pl. XLIII., Figs. 19 and 20).

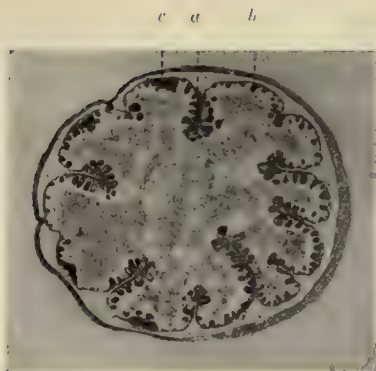


FIG. 15.

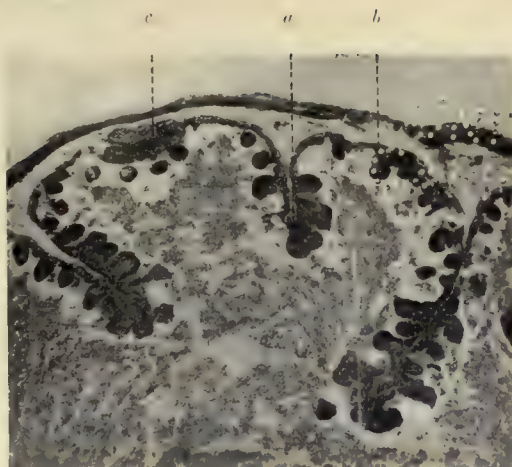


FIG. 16.

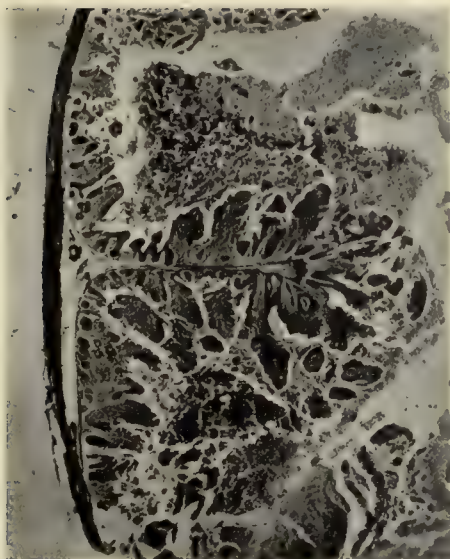


FIG. 17.

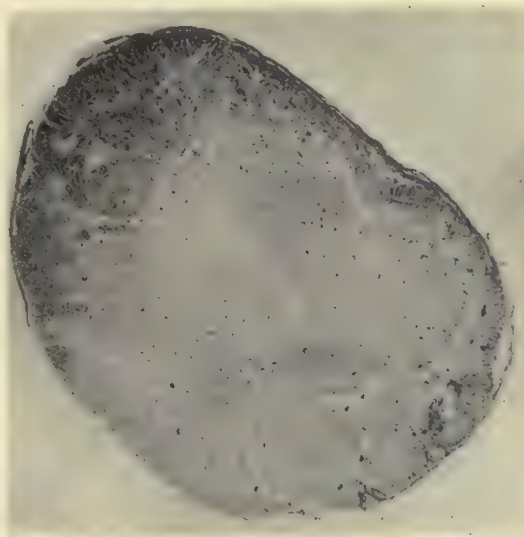


FIG. 18.

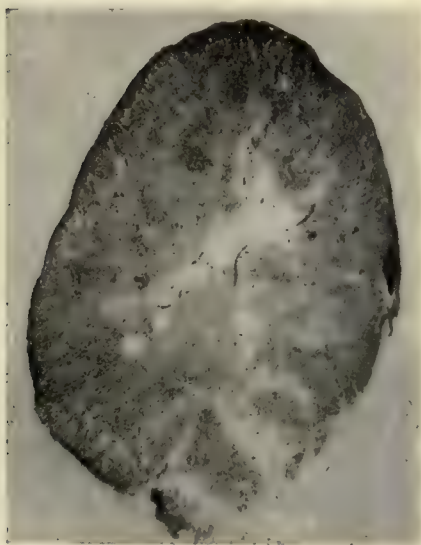


FIG. 19.

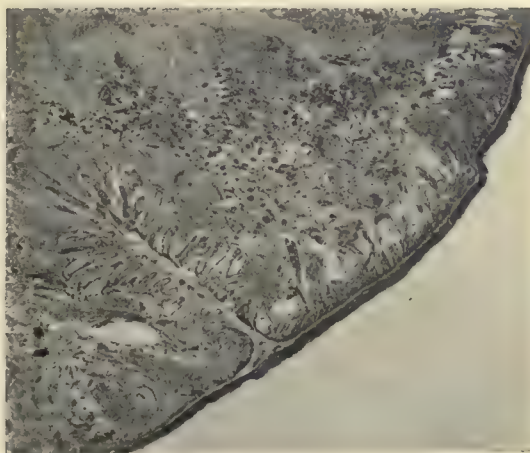


FIG. 20.

SECTIONS OF CÆCUM.

- FIG. 15. ($\times 9$) showing a transverse section of the caecum of a normal Grouse (No. 81). The ridges (*a*) and villi (*b*) are well shown, and three collections of lymphoid tissue (*c*) are also seen.
- FIG. 16. ($\times 25$) showing a portion of the same section more highly magnified.
- FIG. 17. ($\times 25$) showing a portion of a section of the caecum of an apparently healthy wild Grouse (No. 69).
- FIG. 18. ($\times 9$) showing a transverse section of the caecum of a diseased Grouse (No. 2).
- FIG. 19. ($\times 9$) showing a transverse section of the caecum of a diseased Grouse (No. 15) very badly infected with *Strongyli*.
- FIG. 20. ($\times 25$) showing a portion of Fig. 19 more highly magnified. Large numbers of worms are seen in transverse section as black dots.

In fact, the general condition shows evidence of a chronic inflammation leading to fibrosis. Large quantities of mucus are present in the intestinal contents, and the villi appear to be united together with this material, which penetrates to the deepest parts of the crypts between the villi. Everywhere Strongyli are present, and their relationship to the structures composing the wall of the organ is of special interest (Pl. XLIII., Fig. 20). They are found in large numbers both in the lumen and between the villi, in some instances having penetrated to the deepest portions of the crypts. In such cases the epithelium covering the portions of the villi adjacent to the worms is greatly altered, and a marked increase of fibrous tissue in the underlying connective tissue is frequently observed (Pl. XLII., Fig. 12). In some instances the epithelium has completely disappeared all round the worm so that the latter is seen surrounded by a ring of dense fibrous tissue (Pl. XLI., Fig. 10). Occasionally a worm is found lying between the epithelium and the matrix of the villus, which usually shows fibroid change in the neighbourhood (Pl. XLI., Fig. 9).

Evidence of chronic inflammation and fibrosis.

There can be little doubt, therefore, that the presence of the worms in such situations leads to chronic inflammatory changes and fibrosis.

As has already been stated it began to appear probable early in the course of the work that the presence of *Bacillus coli* in the liver and other organs was related in some way to the numbers of Strongyli in the cæca. In several birds which had been raised in captivity in Scotland and subsequently kept in Surrey no Strongyli could be found, even after a careful search, and in their organs there were no bacilli of the colon type (one exception). On the other hand, in the organs of Grouse with very large numbers of Strongyli, *Bacillus coli* was constantly present, either in the liver or in some other organ. In other Grouse with fewer Strongyli *Bacillus coli* was present in some, and appeared to be absent in others.

The relation of *Bacillus coli* in the organs to Strongyli in the cæca.

The results obtained previous to the adoption of the counting method are shown in Table II. (p. 290), in which the birds are arranged in three classes.

[TABLE.

TABLE II.—SHOWING THE RESULTS OF CULTURES PREVIOUS TO THE ADOPTION OF THE METHOD OF COUNTING STRONGYLI.

	Grouse No.	Intestinal worms.			Culture from the organs. ¹			
		Hymenolepis.	Davainea.	Strongylus.	Liver.	Lungs.	Spleen.	Kidney.
Class I. No Strongyli. No <i>B. coli</i> .	5	0	0	...	0	0	0	...
	18	0	0	0	0	0	0	0
	19	0	0	0	0	0	0	0
	21	0	0	0	0	0	0	0
	23	Numerous	Numerous	0	<i>B. coli</i>	0	<i>B. coli</i>	0*
	25	0	0	0	0	0	0	0
Class II. 2 Few Strongyli. <i>B. coli</i> inconstant.	26	0	One	0	0	0	0	0
	16	0	0	Few	...	0
	17	Few	One	Eggs only	0	0	0	0
	30	do.	Numerous	Few	0	0	0	0
	33	Moderate	do.	do.	<i>B. coli</i>	0	0	0
	34	Few	Moderate	do.	0	0	0	0
Class III. Many Strongyli. <i>B. coli</i> constant.	40	0	0	do.	0	0	0	...
	1	Numerous	...	Numerous	<i>B. coli</i>	<i>B. coli</i>
	2	do.	Numerous	do.	do.	0
	3	do.	Few	do.	do.	0
	4	do.	Numerous	do.	do.	0
	6	do.	do.	do.	do.	0
	11	do.	do.	do.	do.	0
	12	do.	do.	do.	do.	0
	13	do.	0	do.	do.	<i>B. coli</i>
	14	do.	0	do.	do.	0
	15	do.	Numerous	do.	do.	<i>B. coli</i>
	22	0	Two	do.	do.	0	0	<i>B. coli</i>
	28	0	0	do.	do.	0	0	0
	29	0	0	do.	do.	0	0	0
	31	Numerous	Few	do.	0	0	<i>B. coli</i>	0
	32	Moderate	Moderate	do.	<i>B. coli</i>	0	0	0
	35	Numerous	Numerous	do.	do.	0	0	0

* Numerous portions of *Davainea* in the caeca.¹ In this and the following Table 0 indicates that no organisms of the *Bacillus coli* type were present in the cultures, and ... that cultures were not made.² In the birds of Class II, the Strongyli were noted as few, but subsequent experience with counting methods showed that what appeared few to an ordinary examination might sometimes turn out to be a hundred or more when counted.

In the birds of Class I. *Bacillus coli* was found once only in the organs, and then in a Grouse with very numerous tapeworms in the duodenum and intestine, and numerous portions of *Davainea* in the caeca, a thing very rarely observed and probably indicating some abnormal condition. *Bacillus coli* was found in the liver of one of six birds belonging to Class II. Amongst the birds belonging to Class III. *Bacillus coli* was constantly

When Strongyli numerous *Bacillus coli* present in organs.

PLATE XLIV.

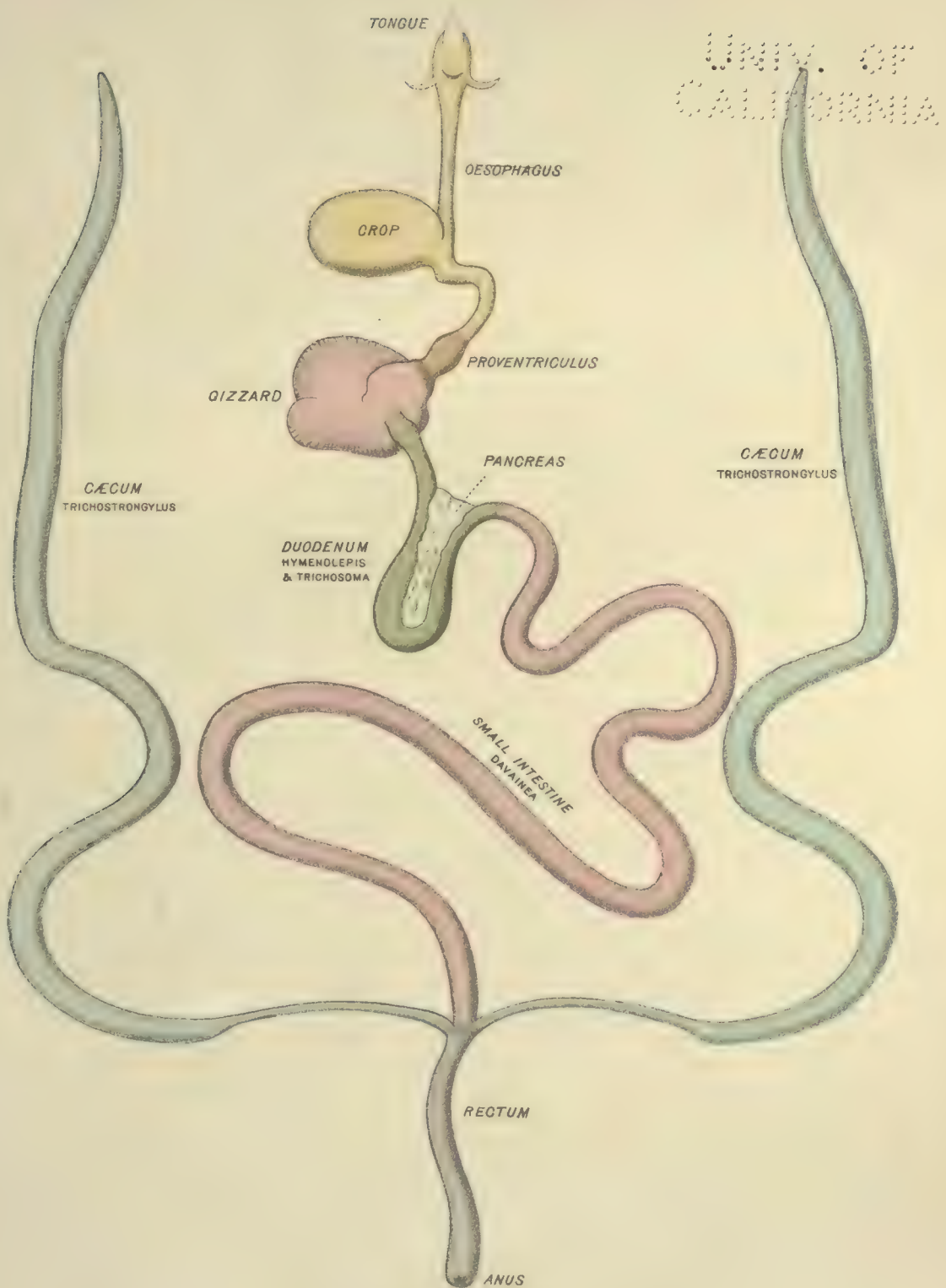


DIAGRAM OF ALIMENTARY CANAL SHOWING HABITATS
OF INTESTINAL PARASITES.

B. Wilson, et al. 1914. Can. J. Zool.

found in the liver (one exception). In five instances they were cultivated from one of the other organs also.

Since the counting of the Strongyli was systematically undertaken twenty-three presumably healthy birds have been examined. The results confirmed the opinions previously arrived at. In this series four birds had less than one hundred Strongyli, and *Bacillus coli* was not found in their organs. Fifteen had Strongyli varying in number between one hundred and one thousand, and *Bacillus coli* was cultivated from the organs of some (eight) and not from those of others (seven). In four birds in which very large numbers of Strongyli, i.e., over one thousand, were counted, *Bacillus coli* was found in the livers of all. The results of these observations are given in the following table.

TABLE III.—SHOWING THE RESULTS OF CULTURES AFTER THE ADOPTION OF THE METHOD OF COUNTING STRONGYLI.

Grouse No.	Number of Strongyli.	Cultures from organs.			
		Liver.	Lungs	Spleen.	Kidneys.
52	0	0	0	0	0
81	0	0	0	0	0
48	32	0	0	0	0
43	45	0	0	0	0
58	113	0	0	0	0
59	235	<i>B. coli</i>	0	0	0
46	259	do.	0	0	0
50	290	do.	<i>B. coli</i>	<i>B. coli</i>	0
49	330	0	0	0	0
47	344	<i>B. ent.</i>	0	<i>B. ent.</i>	0
55	415	0	0	0	0
63	533	0	0	0	0
51	540	<i>B. coli</i>	<i>B. ent.</i>	<i>B. ent.</i>	<i>B. ent.</i>
64	571	0	0	0	0
57	599	<i>B. coli</i>	0	0	0
62	730	do.	0	0	0
67	833	0	0	0	0
44	871	<i>B. coli</i>	0	0	0
66	945	0	0	0	0
54	1645	<i>B. coli</i>	0	<i>B. coli</i>	0
56	1868	do.	<i>B. coli</i>	0	...
60	5995	do.	0	0	0
61	9562	do.	0	0	0

B. ent. = *B. enteritidis*.

The points which come out clearly from these two tables are:—(1) that when Strongyli are absent from the cæca or are present only in small numbers (less than a hundred), intestinal bacteria, especially *Bacillus coli*, are not present in the liver or other organs of the Grouse (eleven

Points brought out by tables.

Grouse—one exception); (2) that a moderate number of Strongyli are present (one hundred to one thousand), *Bacillus coli* may or may not be present in the organs (twenty-one Grouse); and (3) that when great numbers (over one thousand) are present, *Bacillus coli* has invariably been found in the liver or other organs (twenty Grouse.)

It has not been found possible to estimate the numbers of living *Bacillus coli* present from the number of colonies which grew on the tubes. Sometimes, of course, we were able to make a rough guess. In some control birds, both diseased and healthy, which were examined some considerable time after death, the innumerable number of colonies on the tubes showed that *Bacillus coli* was at that time swarming in the tissues. But with living birds, even when very large numbers of Strongyli were present, the colonies of *Bacillus coli* were few in number, one or two to ten or a dozen, and rarely more than thirty.

It is not claimed, of course, that the number of living *Bacillus coli*, in the liver for example, is exactly proportional to the number of Strongyli. Numbers of Strongyli and bacilli not exactly proportional. With as few Strongyli as two hundred and thirty-five, *Bacillus coli* has been found (one colony in one tube), and again with as many as nine hundred and forty-five, *Bacillus coli* has been absent. Doubtless other conditions which affect the health of the bird also influence the permeability of the intestinal wall to the contained bacteria.

We have already shown that Strongyli are almost constantly present in the cæca of wild Grouse believed to be perfectly normal, and certainly of fair weight and in good general condition. In a few so-called healthy birds they may be present literally in thousands. We were informed by Dr Wilson that Strongyli are more numerous in diseased than in healthy birds; and we have ourselves examined a number of diseased birds brought in dead, and useless for cultural purposes, and collected the worms from them. The numbers of Strongyli present in healthy and diseased birds.

Table IV. shows that the number of Strongyli present in diseased birds, though varying considerably, is greatly in excess of that found in the great majority of normal birds. In a small minority of the presumably healthy birds the numbers were as large as those found in many of the diseased birds. It is, of course, impossible to be certain that these exceptional birds were not really suffering from the early stages of "Grouse Disease." The two (Nos. 60 and 61) with the largest numbers came from a moor on which "Grouse Disease" was prevalent at the time. More Strongyli present in diseased than in healthy birds.

The presence in diseased birds of Strongyli in numbers far in excess of those found in normal birds does not of course prove that they were the cause of the disease, because it is conceivable that they may have multiplied as a consequence of the disease. Nevertheless, taken in conjunction with the changes previously described in the mucous membrane of the cæcum, and the relation of the worms thereto, it is exceedingly probable that the worms are really the cause of the disease.

TABLE IV.—SHOWING THE RELATIVE NUMBER OF STRONGYLI IN HEALTHY BIRDS AND IN THOSE BELIEVED TO BE SUFFERING FROM "GROUSE DISEASE."

Birds received alive, apparently in good health, or sent as average specimens of normal Grouse.		Diseased birds picked up dead.		
Grouse No.	Number of Strongyli.	Grouse No.	Number of Strongyli.	
81	0	53	2,506	
52	0	79	2,556	(1,278 in one cæcum)
48	32	74	3,114	(1,557 ")
43	45	78	3,340	(1,670 ")
58	113	74 (a)	3,406	(1,703 ")
59	235	80	3,840	(1,920 ")
46	259	75	4,352	(2,176 ")
50	290	39	6,230	
49	330	71	7,058	(3,529 in one cæcum)
47	344	73	7,484	(3,742 ")
55	415	77	8,800	(4,400 ")
63	533	72	10,266	(5,133 ")
51	540	76	18,332	(9,166 ")
64	571			
57	599			
62	730			
69	730*			
67	833			
44	871			
66	945			
54	1,645			
56	1,868			
70	2,524*			
60	5,995†			
61	9,562†			

* One cæcum only counted and the numbers doubled.

† These birds came from the same moor.

The question arises whether the tapeworms, often present in enormous numbers (Pl. XLII., Figs. 13 and 14) in the gut of the Grouse, act like the Strongyli and increase the permeability of the intestinal wall to bacteria. Tables V. and VI. show that there is little or no relation between the presence of tapeworms in the gut and *Bacillus coli* in the organs, and that numerous tapeworms of either kind, *Hymenolepis*

The relation of *Bacillus coli* in the organs to tapeworms in the intestine.

and *Davainea*, may be present without any *Bacillus coli* appearing in cultures from the liver. On the other hand, *Bacillus coli* may be present in the liver, and yet one or other or both of the tapeworms may be absent.

TABLE V.—SHOWING THAT THE PRESENCE OF HYMENOLEPIS IN THE DUODENUM IS NOT RELATED TO THE PRESENCE OF *BACILLUS COLI* IN THE LIVER.

Grouse No.	Hymenolepis.	Cultures from the organs.			
		Liver.	Lungs.	Spleen.	Kidneys.
52	0	0	0	0	0
81	0	0	0	0	0
48	0	0	0	0	0
43	0	0	0	0	0
49	0	0	0	0	0
58	0	0	0	0	0
55	0	0	0	0	0
59	0	<i>B. coli</i>	0	0	0
46	0	do.	0	0	0
50	0	do.	<i>B. coli</i>	<i>B. coli</i>	0
47	0	<i>B. ent.</i>	0	<i>B. ent.</i>	0
51	0	<i>B. coli</i>	<i>B. ent.</i>	do.	<i>B. ent.</i>
57	0	do.	0	0	0
62	0	do.	0	0	0
44	0	do.	0	0	0
56	0	do.	<i>B. coli</i>	0	0
54	0	do.	0	<i>B. coli</i>	0
60	Few	do.	0	0	0
63	Numerous	0	0	0	0
64	do.	0	0	0	0
67	do.	0	0	0	0
66	do.	0	0	0	0
61	do.	<i>B. coli</i>	0	0	0

B. ent. = *B. enteritidis*.

The great numbers which both these worms may attain is almost unbelievable by one who has not seen them (Pl. XLII., Figs. 13 and 14). *Davainea* seems to be present in the intestine throughout the year. It might appear not without significance that *Hymenolepis*, so numerous from the spring to the autumn months, during which the greatest mortality among Grouse takes place, is scarce or absent during the winter, when the disease is quiescent. On the other hand, we have not observed any gross lesions in the neighbouring mucous membrane even in the worst cases of infection with either of these worms, nor have they, as has already been shown, any relation to the presence of living intestinal bacteria in the tissues. We therefore are not inclined to believe

The prevalence of *Hymenolepis* and *Davainea* in normal and diseased birds.

that they play any part, except perhaps a secondary one, in the causation of "Grouse Disease."

TABLE VI.—SHOWING THAT THE PRESENCE OF *DAVAINEA* IN THE INTESTINE IS NOT RELATED TO THE PRESENCE OF *BACILLUS COLI* IN THE LIVER.

Grouse No.	Davainea.	Cultures from the organs.			
		Liver.	Lungs.	Spleen.	Kidneys.
52	0	0	0	0	0
81	0	0	0	0	0
48	0	0	0	0	0
58	0	0	0	0	0
59	0	<i>B. coli</i>	0	0	0
46	0	do.	0	0	0
50	0	do.	<i>B. coli</i>	<i>B. coli</i>	0
63	0	0	0	0	0
51	0	<i>B. coli</i>	<i>B. ent.</i>	<i>B. ent.</i>	<i>B. ent.</i>
62	0	do.	0	0	0
44	0	do.	0	0	0
43	One	0	0	0	0
66	do.	0	0	0	0
56	Five	<i>B. coli</i>	<i>B. coli</i>	0	0
54	Six	do.	0	<i>B. coli</i>	0
47	Seven	<i>B. ent.</i>	0	<i>B. ent.</i>	0
55	do.	0	0	0	0
57	Eleven	<i>B. coli</i>	0	0	0
67	Moderate	0	0	0	0
49	do.	0	0	0	0
64	Numerous	0	0	0	0
60	do.	<i>B. coli</i>	0	0	0
61	do.	do.	0	0	0

B. ent. = *B. enteritidis*.

In the above tables the birds are arranged in order, according to the number of tape-worms present. When two or more birds had the same number of these worms they are arranged according to the number of Strongyli.

Three Grouse chicks, reared at Frimley and experimentally fed on coccidia by Dr Wilson, were examined by cultures for the presence of intestinal organisms in their organs.

The first (B. 15. Hatched 28.6.09. Fæces examined and no spores of coccidia found. Fed twice on 9.7.09 and 17.7.09 with fæces from other birds containing spores of coccidia. Killed 6.8.09) was very ill and extremely emaciated when received, and was killed and examined immediately. An organism of the *Bacillus enteritidis* type was found in the liver, but not in the other organs. No worms of any

The relation of *Bacillus coli* in the liver to Coccidiosis of the intestine.

kind were found in the intestine or cæca. Sections of the gut examined by Dr Fantham showed numerous coccidia in all stages of multiplication in the epithelial cells. The second chick (B. 2. Hatched at the same time and treated in the same way) was also ill when received, and was killed and examined immediately. In this case a few colonies of *Bacillus coli* were obtained from the liver cultures. No worms were found, and the condition of the intestine was the same as in the first chick. A third older chick (four months) which had been fed on coccidia three weeks previously was also killed and examined. A few streptothrices developed on the cultures from the lungs, but those from the other organs remained sterile. Neither worms nor coccidia were found in the intestine or cæca.

These observations seem to indicate that intestinal Coccidiosis may so injure the gut that bacteria are allowed to pass into the circulation. This conclusion is supported by eight observations on young rabbits suffering from naturally acquired Coccidiosis of the intestine, the results of which are given in the following Table.

TABLE VII.—SHOWING THE RESULTS OF CULTURES FROM THE ORGANS OF YOUNG RABBITS SUFFERING FROM COCCIDIOSIS.

Rabbit No.	Coccidiosis.		Cultures from the organs.						Mesenteric gland.	
	Intestine.	Liver.	Liver.	Spleen.	Lungs.	Kidneys	Blood.	Bile.		
1.	No lesions	Well marked	0	0	0	0	0	0	<i>B. coli</i>	No nematodes.
2.	"	Excessive	0	0	0	0	"	"
3.	"	Well marked	0	0	0	0	"	"
4.	Trace only	Few small spots	0	0	0	0	0	...	"	Many nematodes.
5.	"	"	0	0	0	0	0	...	"	" (233).
6.	Well marked	"	<i>B. coli</i>	0	0	0	"	" (246).
7.	"	One spot	<i>B. ent.</i>	<i>B. enteritidis</i>	0	0	<i>B. coli</i> <i>B. ent.</i> <i>B. coli</i>	No nematodes.
8.	"	Well marked	<i>B. coli</i>	0	0	0	0	...		

B. ent. = *B. enteritidis*.

The mesenteric glands yielded intestinal bacteria in all cases. The cultures from the other organs, including the liver, yielded no intestinal bacteria when the small intestine was normal, or showed merely a trace of Coccidiosis. On the other hand, when the small intestine showed well-marked Coccidiosis *Bacillus coli* or *Bacillus enteritidis* was always present in the liver, and sometimes in the other organs. Thus the existence of Coccidiosis

would seem to allow of intestinal organisms of the colon group to gain entrance into the portal blood. The existence of Coccidiosis of the liver bore no relation to the presence of *Bacillus coli* in that organ, even the affected bile ducts being sterile. The presence of the nematode, *Oxyuris ambigua* in the cæcum (in moderate numbers) did not appear to have any influence on the passage of bacteria from the intestine into the blood-vessels.

We have shown that *Bacillus coli* is constantly present in the organs of birds whose cæca contain large numbers of Strongyli, and we have shown that the latter are present in far larger numbers in diseased than in healthy birds. It may therefore be assumed that *Bacillus coli*, while not invariably absent from the organs of the apparently healthy bird, is constantly present in those of diseased birds. The small numbers of colonies of *Bacillus coli* cultivated from the tissues of diseased Grouse indicate that these bacteria do not multiply in the tissues. We therefore do not suggest that "Grouse Disease" is essentially an infection with these bacteria. But the number of colonies which appear on our tubes does not allow us to estimate even approximately the numbers of bacilli which enter the tissues and get killed. If these are really numerous, their products will doubtless exert some amount of harmful influence, but how much we are not at present in a position to say. No bacilli could with certainty be identified either in sections or in smears of the livers of diseased or healthy birds. Many of the cells were filled with large numbers of iron-containing granules, which seemed to be more numerous in diseased than in healthy birds. But the fact that we have not found either by macroscopic or microscopic examination any important lesions in the livers which have yielded cultures inclines us to think that the bacilli play only a secondary part in the causation of death.

Significance of *Bacillus coli* in the organs.

Though this subject is being very fully dealt with by other workers for the "Grouse Disease" Inquiry we feel that it is desirable, in view of the statements we have made, to record our own observations in tabular form. Though unfortunately we seldom had the opportunity of making observations on diseased and healthy birds at the same time, the table shows that *Hymenolepis microps* occurred in large numbers in the great majority of birds examined from the middle of March to the end of May. Very few were present in the thirteen birds examined between the beginning of June and the last week in August. During the last few days

Seasonal prevalence of the principal Grouse entozoa.

TABLE VIII.—SHOWING THE SEASONAL PREVALENCE OF THE PRINCIPAL GROUSE ENTOZOA.

APPARENTLY HEALTHY BIRDS. Hand-reared, shot, or caught by keepers as examples of healthy birds.					DISEASED BIRDS. Picked up dead on the moors or caught in a weak condition.			
Date.	No.	Hymenolepis.	Davainea.	Strongylus.	No.	Hymenolepis.	Davainea.	Strongylus.
Feb. 3, 1909	54	0	1	1,645
" 5	55	0	7	415
" 5	56	0	5	1,868
" 5	57	0	11	599
" 6	58	0	0	113
" 6	59	0	0	235
Mar. 17	60	Few	Numerous	5,995
" 19	61	Numerous	"	9,562
" 19	62	0	0	730
" 20	63	Numerous	0	533
" 20	64	"	Many	571
" 20	65	"	2	183
" 20	66	"	1	945
" 30	67	"	Moderate	833
April 22	68	Few	0	877
" 27	69	Numerous	Numerous	730*
" 70	70	"	"	2,524*
May 10	71	Numerous	0	7,058
" 5, 1908	72	"	Numerous	10,266*
" 5, 1908	1	"	Numerous	Numerous
" 5, 1908	2	"	Numerous	"
" 5, 1908	3	"	Few	"
" 5, 1908	4	"	Numerous	"
" 5, 1908	6	"	"	"
" 5, 1908	73	"	Fragments	7,484
" 5, 1908	11	"	Numerous	Numerous
" 5, 1908	12	"	"	"
" 5, 1908	13	"	0	"
" 5, 1908	14	"	0	"
" 5, 1908	15	"	Numerous	"
" 5, 1908	74	"	Moderate	3,114*
" 5, 1908	74(a)	Numerous	0	3,406
" 5, 1908	75	"	Numerous	4,352
" 5, 1908	76	"	"	18,332*
" 5, 1908	77	Numerous	0	8,800
" 5, 1908	78	"	Few	3,340
June 3, 1909	16	0	0	Few	79	Few	0	2,556
July 10, 1908	17	Few	1	Few	80	0	0	3,840
" 18	18	0	0	0
" 19	19	0	0	0
" 28	20	0	0	Few
Aug. 5, 1908	21	0	0	0
" 10	22	0	2	Numerous
" 15	23	Numerous	Numerous	0
" 18	25	0	0	0
" 26	26	0	1	0
" 26	28	0	0	Numerous	29	0	0	Numerous
" 30	30	Few	Numerous	Few
" 31	31	Numerous	Few	Numerous
" 32	32	Moderate	Moderate	Moderate
" 33	33	Numerous	Numerous	Few
" 34	34	Few	Moderate	"	35	Numerous	Numerous	Numerous
Sept. 2, 1908	36	0	0	0
" 14	37	0	0	0
Oct. 23, 1908	38	0	Numerous	Numerous	39	Few	Many	6,230
" 28	40	0	0	Few	41	0	Moderate	Numerous
Dec. 8, 1908	43	0	1	45
" 9	44	0	0	871	45	0	Moderate	Numerous
" 9	46	0	0	259
" 9	47	0	0	344
" 9	48	0	0	32
" 9	49	0	Several	330
" 9	50	0	0	290
" 9	51	0	0	540
" 17, 1909	81	0	0	0
" 21, 1908	52	0	0	0

* The Strongyli in one caecum counted and number found doubled.

in August they were met with in moderate numbers in all the birds examined. From the beginning of September to the beginning of February they were absent from all the birds examined with one exception. The relation to season is much less marked in the case of *Davainea urogalli*, though it occurred in the greatest numbers at the same seasons as *Hymenolepis*.

With regard to *Trichostrongylus pergracilis* it is difficult to come to any definite conclusion as to its seasonal prevalence from our own observations, conducted as they were on diseased birds at one time of year, and on healthy, often hand-reared, birds at another; but it is clear that they do not disappear at any season.

The causes of death in the Grouse are, of course, various. We ourselves have seen pleuro-pneumonia (in a bird long kept in captivity in Cambridge), pericarditis, necrotic patches in the liver, an obscure chronic disease of the peritoneum, and septic infection from a gangrenous fracture of the wing. On the other hand, the great majority of birds, either picked up dead on the moor, or caught by keepers when weak and unable to fly, have been found to be all more or less in the same condition; they were wasted, badly infested with *Trichostrongylus pergracilis*, and often with *Davainea urogalli* or *Hymenolepis microps*, or with both. More or less pathological change was seen in the cæca; the mucous membrane was often reddened, and under the binocular microscope considerable changes were seen, though we did not observe gross ulceration. Sections examined under the higher powers showed chronic inflammatory changes of a serious kind, particularly in the immediate neighbourhood of the worms.

Birds showing these changes we take to be representative of those suffering from the chronic form of "Grouse Disease." Whether there be also an acute epizootic disease among Grouse we cannot tell. We can only say that, so far as our experience goes, we have not seen it. We have never seen pneumonia in the wild bird, and we have never seen any birds picked up dead when plump and in good condition without finding evidence that they had died of injury.

No case of acute "Grouse Disease" observed.

We have therefore to discuss the causes of death in the chronic wasting disease, which is observed among Grouse fairly regularly in the spring and to a lesser extent in the autumn, and it is to this we refer when we speak of "Grouse Disease."

First we must consider the gross intestinal parasites which occur in such

remarkable numbers in the Grouse. The tapeworm *Hymenolepis microps* alone of these shows any relation in its seasonal prevalence to "Grouse Disease." This worm, according to our experience, is undoubtedly very numerous in the spring and autumn, the seasons when "Grouse Disease" is most frequently observed,¹ and practically disappears from the bird during the winter months. On the other hand, it has not appeared to be more numerous in diseased than in healthy birds.

Davainea not infrequently occurs in such enormous masses as to distend the gut.

Neither of these tapeworms has been found associated with any constant or serious lesions. *Davainea* appears to us to be the less objectionable. *Hymenolepis*, whose seasonal prevalence more closely agrees with that of "Grouse Disease," seems to us more likely to be harmful. The large masses in which it often exists in the narrow duodenum appear not unlikely to interfere mechanically with the free passage of food material. Both worms probably make a considerable demand for their own sustenance, even if they do not exert a more serious injurious influence.

The case against the nematode, *Trichostrongylus pergracilis*, is much clearer, for though it is seldom entirely absent from healthy birds, nevertheless, definite lesions in the cæcum are often associated with its presence in large numbers. It probably, however, does little harm if not too numerous. With regard to the presence of this parasite in large numbers in some of the birds caught on the moor, and supposed to be normal birds, it must be remembered that strong wild Grouse are difficult to catch, and that some at least of the methods of capturing Grouse alive seem calculated to catch the weakest birds rather than the stronger ones. On the other hand, we have counted the Strongyli in a number of "normal" and diseased birds, and have found, on the whole, a great difference between the two classes; very large numbers being always found in the diseased birds, much larger indeed than those found in all but the exceptional members of the healthy class; and these, for reasons just stated, may perhaps be not normal at all but suffering from the early stages of "Grouse Disease."

These nematodes, in birds picked up dead or brought to us by the keepers as suffering from "Grouse Disease," are, so far as our experience goes, almost

¹ It is questionable whether there is ever a true outbreak of "Grouse Disease" except in the spring. Sickly birds observed in August and September are now believed to be birds recovering from the spring outbreak, *vide* chap. iii. p. 49, chap. v. p. 128.

always associated with grave changes in the mucous membrane of the cæcum; and concurrently with these changes intestinal bacteria, particularly those belonging to the *Bacillus coli* group, find their way into the liver, or even into the other organs. We have determined by actual worm counts and cultures that *Bacillus coli* is always absent from the liver (in birds examined immediately after death) when there are no Strongyli (hand-reared birds) or only very few (not exceeding one hundred in number). When more than one hundred but less than one thousand are found, *Bacillus coli* is sometimes present in, and sometimes absent from, the organs, but when the numbers of Strongyli exceed one thousand, then *Bacillus coli* is always present in the liver, and occasionally in the other organs.

We have not been able to satisfy ourselves that the bacilli which find their way into the organs do much harm. Some harm no doubt they do, but how much we cannot say. Microscopic examination has not revealed any profound changes in these livers. The numbers in which these bacteria penetrate into the organs is difficult to estimate because, doubtless, they soon get killed in the living tissues, so that the numbers of colonies cultivated must bear only a small proportion to the total number of bacteria which have entered the fragment of tissue examined. The number of *living* bacilli in the organs of these Grouse is undoubtedly small; from which it is evident that they do not multiply in the organs. "Grouse Disease" is therefore not an *infection* with these bacteria. Is it a toxæmia caused by the poison liberated from bacteria which have been absorbed from the intestine, and which have almost immediately perished in the tissue? We know that in order to produce serious mischief in animals by a single injection of dead bacteria a considerable quantity must be employed; and it is difficult to believe, when we remember the small numbers of colonies which grew on our cultures, that relatively to this quantity the numbers of bacteria absorbed could have been very large. On the other hand, we have little information concerning the influence of the constant absorption of small numbers of bacteria, but this is believed by Adami and his school to be a potent source of disease. The fact that we have repeatedly found *Bacillus coli* in the livers of "normal" birds badly infected with Strongyli, prevents us from ascribing the death of the Grouse directly to these bacilli, though they probably play some part.

It seems to us quite certain that the Strongylus when exceptionally numerous

injures the mucous membrane of the cæca, and that this injury allows of the absorption of certain intestinal micro-organisms into the portal blood. It doubtless allows also of the absorption of other substances of an irritating or poisonous nature, and probably interferes with the normal selective absorption of nourishment. If we are right in thinking that the cæcal contents become partly retained, and stick to the absorbing surfaces of the ridges of the mucous membrane, we have still more reason to believe that nutrition is greatly interfered with.

“Grouse Disease,” as we see it, appears to us not to be a specific bacterial infection. We conceive that all the birds which are more or less severely affected by *Strongyli* suffer injury from this cause to an extent which is more or less proportional to the severity of the infection. Some exceptionally strong birds may stand a larger infection better than weaker birds will stand a lesser; but, on the whole, the birds with the largest numbers of *Strongyli* suffer most. Their nutrition is impaired owing to interference with the normal absorption of digested food, and to the abnormal absorption of soluble poisons and intestinal bacteria. Such birds become the weakest; and when food becomes scarce, as it does at the beginning of spring, especially after bad winters or on overstocked moors, or when other harmful influences prevail, it is the weakest birds which suffer most. They die of privation acting on a constitution already weakened by the consequences of *Strongylosis*, while their stronger neighbours manage to pick up a living somehow, and tide over the period of distress.

TABLE IX
SUMMARY OF ALL OBSERVATIONS

TABLE IX.—SUMMARY OF ALL OBSERVATIONS.

Trichostrongylus pergracilis.

In Grouse Nos. 1-41 the Strongyli were not counted, and only portions of the caecal contents were examined.

In Grouse Nos. 43-68 (except 45) the Strongyli were counted in both caeca separately (see p. 12).

In Grouse Nos. 69-81 (indicated * in Table) the Strongyli were counted in one caecum and the number found doubled.

No.	Date.	Locality and History.		Sex.	Weight in ozs.	Intestinal Worms.			Cultures from Organs.
						Hymenolepis.	Davainea.	Strongylus.	Liver.
1	5.5.08	Inverness.	Caught unable to fly	♂	16	Numerous	...	Numerous	<i>B. coli</i> (12)
2	6.5.08	do.	do.	♂	16	do.	Numerous	do.	<i>B. coli</i> (several)
3	6.5.08	do.	do.	♂	...	do.	Few	do.	<i>B. coli</i> (12)
4	6.5.08	do.	do.	♂	20	do.	Numerous	do.	<i>B. coli</i> (few)
5	7.5.08	Normal hand-reared bird. Frimley		...	15	0	0	...	0
6	7.5.08	Inverness.	Caught unable to fly	♂	16	Numerous	Numerous	Numerous	<i>B. coli</i> (several)
11	9.5.08	do.	do.	♂	17	do.	do.	do.	<i>B. coli</i> (several)
12	9.5.08	do.	do.	♀	...	do.	do.	do.	<i>B. coli</i> (few)
13	9.5.08	do.	do.	♀	18	do.	0	do.	<i>B. coli</i> (1)
14	9.5.08	do.	do.	♂	16	do.	0	do.	<i>B. coli</i> (1) <i>st.c</i>
15	9.5.08	do.	do.	♂	23	do.	Numerous	do.	<i>B. coli</i> (several)
16	2.6.08	Normal.	Frimley	♂	15	0	0	Few	...
17	10.7.08	do.	do.	♂	14	Few	1	Eggs only	<i>sb</i>
18	10.7.08	do.	do.	♂	21	0	0	0	<i>sb</i>
19	24.7.08	do.	do.	♀	23	0	0	0	0
20	28.7.08	do.	do.	...	15	0	0	Few	...
21	5.8.08	do.	do.	♀	15	0	0	0	0
22	10.8.08	do.	do.	♀	...	0	2	Numerous	<i>B. coli</i> (1)
23	15.8.08	Inverness.	Apparently healthy	♂	13	Numerous	Numerous	0	<i>B. coli</i> (4)
25	18.8.08	Normal.	Frimley.	♂	15	0	0	0	0
26	18.8.08	do.	do.	♀	13	0	1	0	<i>S. Lutea</i> (1)
28	...	Inverness	0	0	Numerous	<i>B. coli</i> (few)
29	27.8.08	Inverness.	Caught unable to fly	...	15	0	0	do.	<i>B. coli</i> (1)
30	26.8.08	Inverness.	Apparently healthy	♀	16	Few	Numerous	Few	0
31	27.8.08	do.	do.	♀	20	Numerous	Few	Numerous	0
32	28.8.08	Inverness.	Healthy, caught on moor	♀	16	Moderate	Moderate	Moderate	<i>B. coli</i> (2)
33	28.8.08	do.	do.	♂	15	Numerous	Numerous	Few	<i>B. coli</i> (few)
34	29.8.08	do.	do.	♂	18	Few	Moderate	do.	0
35	29.8.08	Nairn.	Caught on moor. Ill	♀	17	Numerous	Numerous	Numerous	<i>B. coli</i> (several)
36	3.9.08	Normal bird.	Examined four days after death	♀	...	0	0	0	...
37	14.9.08	Normal bird.	Found dead. Frimley	♀	11	0	0	0	...
38	23.10.08	Normal bird.	Died of pericarditis	♂	20	0	Numerous	Numerous	<i>st.c</i> (1)

TABLE IX.—*continued.*

B. enter.—Bacillus of the *B. enteritidis* group.
c=coccus.
m=mould.

sb=spore-bearing bacillus.
sz=streptothrix.
b=bacillus.

d=diphtheroid bacillus.
s=sarcina.
st.c=streptococcus.

The numbers or words in brackets indicate the number of colonies found.

Cultures from Organs.								Remarks.
Lungs.		Kidneys.		Spleen.	Pancreas.	Bile.	Blood.	
Right.	Left.	Right.	Left.					
<i>B. coli</i> (1)	0	Examined two hours after death. Moderate reddening of caecal villi.
<i>d</i> (3)	0	Caecal mucous membrane much congested.
0	0	Caecal mucous membrane little congested.
0	<i>st.c</i> (2)	Caecal mucous membrane not congested.
0	0	do. do.
0	0
<i>m</i> (1)	<i>b</i>	Caecal mucous membrane much congested.
0	0	Caecal mucous membranes slightly congested.
<i>B. coli</i>	Caecal mucous membrane not congested.
0	0	do. do.
<i>B. coli</i>	<i>B. coli</i>	Caecal mucous membrane extremely congested.
0	Caecal mucous membrane not congested. Gut wounded while making cultures.
<i>sz, sb</i>	<i>sz, sb</i>	<i>sb</i>	<i>sb</i>	<i>sb, m</i>	...	0	0	Caecal mucous membrane not congested.
<i>sb</i>	<i>sb</i>	<i>sz</i>	0	0	...	<i>sb</i>	0	do. do.
0	0	0	0	<i>sb</i> (1)	...	0	0	...
0	0	0	0	Gut wounded when making cultures.
<i>m</i> (1), <i>sb</i> (1)	0	0	0	0	...	0
<i>sb</i> (1)	<i>m</i> (1)	<i>B. coli</i> (2)	0	0	...	0
	<i>c</i> (1)							
0	<i>m</i> (1)	<i>sb</i> (1)	0	<i>B. coli</i> (1)	...	0	...	Numerous proportions of <i>Darvainea</i> in caeca.
<i>m, sz</i>	<i>m, sb</i>	0	<i>c</i> (1)	0	...	0
<i>m</i> (1), <i>d</i> (1)	<i>m</i> (1)	0	0	0	...	0
	<i>sz</i> (1)							
<i>m</i> (2)	<i>sb</i>	0	0	0	<i>c</i> (1)	Shot in wing. Brought in alive.
<i>m, sz</i>	<i>sz</i> (1)	0	0	0
<i>m</i> (1)	<i>m</i> (1)	<i>sb</i> (1)	0	0
<i>m</i> (1), <i>sb</i> (1)	<i>m</i> (1), <i>sb</i>	0	0	<i>B. coli</i> (1)
<i>m</i> (3)	<i>m</i> (1)	<i>sb</i> (1)	0	0
0	<i>sb</i> (1)	0	0	<i>s</i> (1)
0	0	<i>sb</i> (1)	0	0
0	<i>b</i> (1)	0	0	0	0	Caecal mucous membrane somewhat reddened.
...
...
0	0	0	0

TABLE IX.—*continued.*

No.	Date.	Locality and History.	Sex.	Weight in ozs.	Intestinal Worms.			Cultures from Organs.
					Hymenolepis.	Devainea.	Strongylus.	Liver.
39	24.10.08	Lancashire. Caught unable to fly	♂	18	Few	Numerous	6,230	...
40	28.10.08	Normal. Died of pneumonia. Frimley	♂	20	0	0	Few	0
41	28.10.08	Lancashire. Caught unable to fly	♂	20	0	Moderate	Numerous	...
43	8.12.08	Cumberland. Normal	♂	17	0	1	45	0
44	8.12.08	do. do.	♀	19	0	0	871	<i>B. coli</i> (4)
45	8.12.08	Nairn. Picked up dead	♂	16	0	Moderate	Numerous	...
46	8.12.08	Cumberland. Normal	♂	16	0	0	259	<i>B. coli</i> (1)
47	9.12.08	do. do.	...	18	0	0	344	<i>B. enter</i> (several)
48	9.12.08	do. do.	♂	...	0	0	32	s (2)
49	9.12.08	do. do.	♀	13	0	Several	330	c (1)
50	9.12.08	do. do.	♀	19	0	0	290	<i>B. coli</i> (3)
51	9.12.08	do. do.	♀	13	0	0	540	<i>B. coli</i> (many)
52	21.12.08	Lancashire. Normal. Hand-reared	♂	15	0	0	0	0
53	...	Montgomeryshire. Picked up dead	♂	16	0	0	2,506	...
54	3.2.09	Cumberland. Normal	♀	16	0	6	1,645	<i>B. coli</i> (several)
55	3.2.09	do. do.	♀	17	0	7	415	0
56	5.2.09	do. do.	♂	16	0	5	1,868	<i>B. coli</i> (many)
57	5.2.09	do. do.	♀	17	0	11	599	<i>B. coli</i> (several)
58	5.2.09	do. do.	♀	17	0	0	113	0
59	6.2.09	do. do.	♀	12	0	0	235	<i>B. coli</i> (several)
60	17.3.09	Yorkshire. Normal. Caught on moor	♀	21	Few	Numerous	5,995	<i>B. coli</i> (several)
61	17.3.09	do. do.	...	21	Numerous	Numerous	9,562	<i>B. coli</i> (several)
62	19.3.09	do. do.	♀	21	0	0	730	<i>B. coli</i> (8)
63	20.3.09	Selkirk. Normal. Caught on moor	♀	18	Numerous	0	533	c (1)
64	20.3.09	do. do.	♀	20	do.	Numerous	571	0
65	20.3.09	Cumberland. Shot.	♀	18	do.	2	183	...
66	20.3.09	Selkirk. Normal. Caught on moor.	♀	19	do.	1	945	0
67	20.3.09	do. do.	♀	18	do.	Moderate	833	0
68	22.4.09	Caithness. Normal. Caught on moor	♀	16	0	0	877	...
69	27.4.09	Inverness. Normal. Caught on moor.	♂	23	Numerous	Numerous	730*	...
70	27.4.09	do. do.	...	23	do.	do.	2,524*	...
71	10.5.09	Inverness. Caught, unable to fly	♀	16	do.	0	7,058*	...
72	10.5.09	Inverness. Picked up dead	♂	17	do.	Numerous	10,266*	...
73	7.5.09	Nairn. Picked up dead	♀	17	do.	Fragments	7,484*	...
74	21.5.09	Yorkshire. Picked up dead	♀	17	0	Moderate	3,114*	...
74a	21.5.09	do. do.	Numerous	0	3,406*	...
75	19.5.09	do. do.	♂	...	do.	Numerous	4,352*	...
76	19.5.09	Lancashire. Picked up dead	0	do.	18,332*	...
77	19.5.09	Selkirk. Picked up dead	♀	21	Numerous	0	8,800*	...
78	24.5.09	do. do.	♀	16	do.	Few	3,340*	...
79	3.6.09	Inverness. Picked up dead.	♀	17	Few	0	2,556*	...
80	3.6.09	do. do.	♀	19	0	0	3,840*	...
81	17.12.09	Normal. Frimley	♀	15	0	0	0	0

TABLE IX.—*continued.*

[illegible]

CHAPTER XIII

OBSERVATIONS ON THE BLOOD OF GROUSE¹

By Dr H. B. Fantham

INTRODUCTION

THE elements of the blood of birds are very different from those of mammals, and while much is known of the histology of mammalian blood, the investigation of the blood of birds has hitherto been very limited, and very little indeed is known of the subject. Such literature as is available on avian blood is, unfortunately, largely contradictory, and the few illustrations relating to the same have not solved entirely the difficulties connected with the cellular elements of the blood of birds.

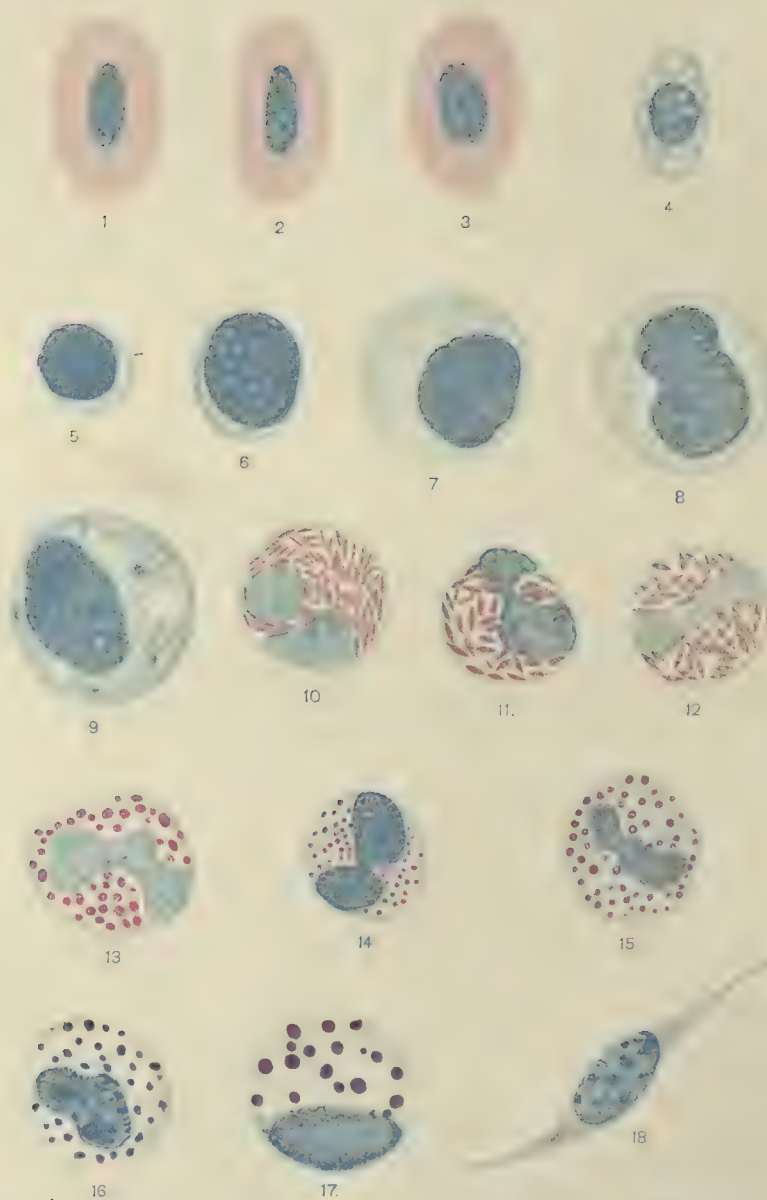
The portions of the subject that have been most adequately dealt with are those relating to certain pathological conditions, fowl cholera and fowl typhoid occurring in domestic fowls, and those relating to normal fowls' blood. In connection with both these sets of observations there are wide discrepancies between the results obtained by different investigators, and much confusion has arisen therefrom.

The different results obtained by various investigators are partly explicable, for the constitution of the blood of birds may vary among individuals of the same species. Also there are differences due to age and sex, while the conditions under which the investigations are made have some influence on the result.

The chief difficulties of manipulation for the investigation of the blood of such birds as Grouse are the rapidity with which coagulation occurs, and the rapid alteration and disintegration that often follows the death of the blood elements. The great rapidity of the onset of degeneration in the leucocytes is such that extreme accuracy in counts of these cellular elements is not easily obtained, and the numbers of erythrocytes and leucocytes found in different series of counts consequently bear a varying relation one to another in apparently normal birds,

¹ Reprinted from the *Proceedings of the Zoological Society of London*, 1910.

PLATE XLV.



BLOOD CELLS OF BIRDS.

even when the factors noted in the preceding paragraph have been considered. Nevertheless, the correlation of the numbers and condition of the blood-elements, particularly of the leucocytes, with the occurrence of specific protozoal and helminthic parasites, renders an examination of the blood a most useful adjunct in investigating somewhat obscure diseases. Several protozoal parasites (*vide* chapter xiv. p. 318), are present in Grouse, both in the blood and in the gut, and the condition of the bird's blood can be correlated with the presence of some of the individual parasites.

Blood taken from a wing vein was used in the case of living birds, of which twelve were thus examined. In the case of freshly killed Grouse, blood taken directly from the heart was employed. The usual methods and precautions were followed in securing suitable drops of blood for examination. Methods.

Hayem's fluid was used as a diluent for counting the red cells of the blood, while Toison's fluid was used in the case of the leucocytes.

The Thoma-Zeiss hæmocyto-meter was employed. The disc of the counting chamber was ruled according to Zappert.

A dilution of at least 200 or 250 was found to be necessary for counting the red cells, and a dilution of 20 to 25 was absolutely necessary in counting the leucocytes. Sometimes a dilution of 100 was taken in counting the leucocytes, and this greater dilution was often preferable.

For differential leucocyte-counts blood-smears were made on both cover-slips and slides, especially the former.

The stain generally used in making preparations for differential counting was that of Jenner. Occasionally Giemsa's stain was employed.

The elements present in the blood of normal Grouse may be grouped as:

- | | |
|-------------------|------------------------------|
| (a) Erythrocytes. | Cells in
normal
blood. |
| (b) Leucocytes. | |
| (c) Thrombocytes. | |

The leucocytes are further subdivided, and may be grouped as mononuclear, polymorphonuclear, and eosinophile leucocytes, and lymphocytes. Mast cells, which are markedly basophile, are also present. Erythroblasts also may be encountered. These forms may now be considered separately.

(a) *Erythrocytes*.—These are the most abundant elements in the blood. The erythrocytes or red blood corpuscles are oval in contour (Pl. XLV., Fig. 1). They

possess a well-marked oval nucleus, centrally placed. The erythrocytes of Grouse are about 11.5μ to 12μ long by 7μ to 7.5μ broad. In fresh preparations the cytoplasm of the red cells of healthy Grouse is practically homogeneous, or but very faintly granular. Stained preparations give the same results. It is rare for large granules, chromatoid granules, or vacuolations to be present in the red cells of healthy birds. The nucleus stains deeply, and shows a well-marked chromatic meshwork with small net-knots upon it at intervals.

The red cells of various birds are much the same. There may be slight differences in size and shape. In Figs. 2 and 3 are depicted stained specimens of the red cells of the pigeon and fowl respectively, from which it will be seen that the erythrocytes of the pigeon are slightly narrower than those of the Grouse and fowl, and somewhat less rounded at the ends.

The number of red cells of Grouse varied from 3,600,000 to 5,800,000 per cubic millimetre, averaging 4,300,000 per cmm. These figures result from blood-counts of fifty birds.

The number of red cells is apparently higher in cock Grouse (*e.g.*, 4,400,000 per cmm.) than in hen Grouse (*e.g.*, 3,800,000 per cmm.).

(b) *Leucocytes*.—The leucocytes of Grouse are a subject of much intrinsic difficulty, and it is impossible to consider the grouping arrangement given below as more than provisional. The classification of the leucocytes of birds can be placed on a really sound basis only when detailed knowledge of the development of *all* the elements of the blood of birds has been obtained. In spite of good work by Denys, Dantschakoff, and others, such a complete developmental investigation of the blood of birds is still wanting. Owing both to the lack of time at my disposal, and to the great scarcity of *quite fresh* material, I am unable to attempt such an investigation, and therefore have availed myself of the classification at present adopted by such authorities as Burnett (1908), modifying their statements in accordance with my own personal observation and adding a number of details hitherto overlooked.

1. *Lymphocytes* (Pl. XLV., Figs. 5, 6).—The lymphocytes are the smallest of the leucocytes. They are from 5.5μ to 8μ in diameter approximately. They are smaller than the average red corpuscles. Each lymphocyte possesses a well-marked round or oval nucleus which is relatively large and occupies most of the cell. The cytoplasm of the lymphocyte is small in amount, is basophile, and is reduced to a rim around the nucleus. The lymphocytes have a great tendency to collect together in groups on blood-smears, and in such aggregations

the cytoplasm of the members away from the periphery of the group is reduced to a minimum.

The lymphocytes are sometimes subdivided into large and small varieties. The larger specimens of lymphocytes gradually merge into the small mononuclears, and the naming and classifying of such leucocytes is often a matter of personal opinion.

2. *Large Mononuclear Leucocytes* (Hyaline cells).—These are large, approximately circular cells averaging 9μ to 11.5μ in diameter (Pl. XLV., Figs. 7, 8). In a film stained with Giemsa's fluid the mononuclear leucocytes are easily distinguishable, not only from their large size, but also from the fact that their cytoplasm stains a vivid blue and the nucleus a beautiful purple. The general cytoplasm of the cell is almost homogeneous in character.

Large
mono-
nuclear
leucocytes.

The nucleus of a mononuclear leucocyte of Grouse is large, occupying about half of the cell, and is often round or oval (Figs. 5, 6). At other times the nucleus is somewhat curved or indented (Fig. 8). The chromatin of the nucleus takes the form of a fairly dense mass, exhibiting in stained specimens a uniformly mottled appearance; it is situated to one side of the cell.

With Jenner's stain the nucleus colours a rather deep blue, while the cytoplasm stains only a faint blue and so is slightly basophile.

As Burnett (1908, p. 35) writes: "One can find all stages between typical lymphocytes with a small amount of strongly basophile, coarsely reticular cytoplasm, and typical large mononuclears with a much larger amount of faintly basophile, finely reticular cytoplasm."

3. *Polymorphonuclear leucocytes* (Burnett) or *Crystalloid eosinophile Cells* (Cullen, Warthin).—The apparently polymorphonuclear leucocytes of birds exhibit marked differences from those of mammals as regards the contained granules.

Polymor-
phonuclear
leucocytes.

These cells in Grouse are round, as seen in stained preparations, and measure from 9μ to 9.5μ in diameter (Figs. 10-12). The nucleus consists of two or more lobes, and varies in shape—in other words, is polymorphous. The nucleus is fairly well stained with Jenner's stain, and is coarsely reticular (Figs. 10-12). The cytoplasm stains very faintly.

Embedded in the general cytoplasm are a number of bodies or granules which stain red with Jenner's stain and are oxyphilic. The bodies are generally described as spindle-shaped with tapering ends, but their outline has also been compared with that of a torpedo or cigar (Fig. 11). Other leucocytes are found with thinner inclusions or "granules" which are rod-like in shape (Fig. 10).

Cullen (1903) writes : " As to the nature and origin of these spindles [inclusions in the cytoplasm of the leucocytes] very little is known that is definite. They are certainly not artifacts, for they can be seen in fresh blood as well as in dried specimens. Dr Simon is of the opinion that they may be derived from the second variety [the coarsely eosinophile leucocytes, mentioned next], in which granules take the place of the spindles ; that they are crystalloids and analogous to similar formations that have been encountered in certain tissues in man, and notably in the epithelial cells of the seminal tubules. He thinks that they result from the granules through loss of water, and as a matter of fact it is possible to reconvert the crystalloids into granules in the wet preparation by adding a droplet of a dilute solution of eosin from the side of the cover-glass. Dr Simon has also noted that in certain preparations in which the eosinophilic material is present in one dense, apparently undifferentiated mass, the crystalloids separate out upon the application of heat."

In a few cases, the centre of the spindle bodies is occupied by a tiny circle or dot, which does not stain as deeply as the rest of the spindle, and is refringent (Fig. 12). The presence of this central dot is noticeable in the case of large spindles.

As regards the staining properties of the spindle bodies (crystalloids), I agree with Burnett that they are not intensely eosinophilic, but that "in affinity for stains the [spindle] granules resemble the polymorphs rather than the eosinophiles." Cullen, on the other hand, considers that the crystalloids are more oxyphilic than the true eosinophile leucocytes. Perhaps the differences of opinion of the various investigators are explicable by reference to slight variation in the stains used.

The distribution of the cytoplasmic inclusions within the cell is dependent on the shape and position of the nucleus.

4. *Eosinophile leucocytes* (Burnett) or *coarsely granular eosinophile (oxyphile) Cells*.—These cells are also present in the blood of normal Grouse (Figs. 13-15), but Eosinophile leucocytes are more numerous in the blood of birds suffering from helminthiasis. The eosinophile cells are from 8μ to 10μ in diameter, and have a general resemblance to the polymorphonuclear leucocytes, only differing in the form of the inclusions or granules.

The shape of the eosinophile leucocyte is round (Figs. 14, 15) or somewhat quadrilateral (Fig. 13). The general cytoplasm is pale staining and slightly reticulate in structure. The nucleus usually resembles that of the polymorphonuclear leucocyte, and is mostly bilobed—the lobes being coarsely reticular and usually staining fairly deeply. The cell-body contains numbers of coarse, oxyphile

(acidophile) granules which stain deeply with eosin. The granules are often rounded (Figs. 13-15); they vary in size, some eosinophiles containing large granules (Fig. 13) which may be relatively fewer in number, while in other cases the granules are small (Fig. 14), and may be relatively more numerous. Eosinophiles with large granules are more prevalent. The contour of the granules is generally round, but sometimes cells containing somewhat ovoid granules are seen which stain intensely with eosin.

Occasionally eosinophile cells are found in stained films, the granules of which vary in shape within the same cell, some being round, some ovoid, and some almost spindle-shaped. Such cells and their contained granules may be somewhat deformed in the making of the film, otherwise it is difficult to classify these cells, which are intermediate between crystalloid (polymorphonuclear) and granular eosinophiles.

Mononuclear eosinophile cells are occasionally seen in the blood of normal Grouse, and perhaps represent an early stage of development of the polymorphonuclear eosinophiles. Such mononuclear cells are somewhat smaller than those depicted in Pl. XLV., Figs. 13-15, and have round nuclei. They are rare, and are perhaps analogous to the young eosinophile myelocytes of man.

5. *Mast Cells* (coarsely granular basophile cells) are present in the blood of normal Grouse (Figs. 16, 17). They are rare. The cells are more or less rounded, with a pale staining cytoplasm. The nucleus is usually rounded (Fig. 17) or slightly polymorphous (Fig. 16), and stains blue with Jenner's stain—rather more deeply than similar cells in mammals. Mast cells.

Basophile granules, which vary in size and in number, occur in the cytoplasm. The granules are usually rounded and stain a deep purplish colour with Jenner's stain—in other words the granules are metachromatic. Mast cells measure from 9μ to 10.5μ in diameter.

(c) *Thrombocytes* also occur in the blood of Grouse (Fig. 4). In the fresh condition they suggest very narrow and slightly small erythrocytes. They are often elliptical, with an oval nucleus centrally placed. Throm-
bocytes.

When stained the cell-body is pale and vacuolated, suggesting a coarsely reticular cytoplasm. The whole cell is basophile in its reactions, staining rather faintly blue with Jenner's stain.

Thrombocytes in Grouse average 9μ by 4μ .

These elements may collect in clumps, and show a marked tendency to degeneration.

Red cells without nuclei were occasionally found in the blood of Grouse. Such non-nucleate cells, however, were very rare.

At times there also appeared to be a number of free nuclei in the blood of Grouse. In this connection we may note that Warthin (1907) found 16·5 per cent. of degenerated cells in the blood of normal fowls.

Erythroblasts occur in the blood of Grouse in small numbers. The cells, which are nucleated, are rounder than erythrocytes, and are devoid of hæmoglobin. The nucleus of an erythroblast is more spherical than that of an erythrocyte. The general cytoplasm is homogeneous, staining blue with Giemsa's stain.

The number of leucocytes found per cubic millimetre in the blood of apparently healthy Grouse varied from 22,000 to 50,000, averaging about 32,000 per cmm.

The average results of the differential counts of leucocytes of apparently healthy Grouse may be tabulated thus :

Lymphocytes	57 per cent.
Large mononuclears	19 „
Polymorphonuclears (crystalloid eosinophiles)	20 „
Eosinophiles (coarsely granular eosinophiles) .	3 „
Mast cells (basophiles)	1 „

The difficult computations are those of the large mononuclears and lymphocytes. There are many medium-sized mononuclears in Grouse, which different observers would classify differently.

The association of altered conditions of the blood with the presence of protozoal parasites has been noted already, and I have found certain alterations in the relative proportions of the blood cells of Grouse that harboured protozoa —Leucocytozoa, Spirochætes and Coccidia—while other differences are to be associated with helminthiasis. The results may now be summarised :

(a) When *Spirochæta lagopodis* (*vide* chapter xiv. p. 323) was present in the blood of Grouse, as it was to some extent in two specimens, the number of mononuclear leucocytes increased, and these leucocytes became slightly enlarged and vacuolated (Pl. XLV., Fig. 9). Levaditi (1901) noticed the presence of vacuolated mononuclear leucocytes in the blood of fowls infected with *Spirochæta gallinarum*, together with mononuclear and polynuclear leucocytosis. Balfour (1908) found vacuolated mononuclear leucocytes in the blood of fowls suffering from spirochætosis in the Soudan. The infection of Grouse with *S. lagopodis* was probably not nearly as great as that of fowls with *S. gallinarum* investigated by Levaditi and Balfour.

(β) The presence of *Leucocytozoon lovati* (*vide* chapter xiv. p. 318) in the blood of Grouse is associated with mononuclear leucocytosis. A differential leucocyte count of the blood of one of the Grouse containing *L. lovati* gave: With *Leucocytozoon lovati*.

Lymphocytes	63.0 per cent.
Large mononuclears	28.0 „
Polymorphonuclears	5.5 „
Eosinophiles	2.5 „
Mast cells	1.0 „

There was also evidence of polychromatophilia in the red cells of Grouse infected with *Leucocytozoon lovati*.

(γ) *Eimeria* (*Coccidium*) *avium* (*vide* chapter xi. p. 235) also has its effect, indirectly, on the blood. Birds suffering from Coccidiosis became anæmic. The paleness of the blood is due to the diminished number of red cells in the blood. Estimations of the hæmoglobin-value by Tallqvist's scale¹ gave With *Eimeria avium*. 60-70 in the case of Grouse chicks suffering from Coccidiosis, 80-90 for healthy Grouse chicks.

There is an increased number of polymorphonuclear leucocytes (crystalloid eosinophiles). Differential leucocyte counts of two Grouse chicks dying from Coccidiosis gave:

Polymorphonuclears	31.5 to 39.5 per cent.
Eosinophiles	3.5 to 5.5 „
Large mononuclears	13.5 to 31.0 „
Lymphocytes	26.0 to 50.0 „
Mast cells	0.6 per cent.

In mammals an increase in the number of polymorphonuclear leucocytes occurs in inflammation, especially locally. The increase in polymorphonuclear leucocytes (crystalloid eosinophiles) is probably to be associated with the intestinal inflammation caused by the presence of coccidian parasites.

Similarly in a fowl chick dying of Coccidiosis, I obtained the following differential leucocyte count:

Polymorphonuclears	47 per cent.
Eosinophiles	2 „
Mononuclears	29.5 „
Lymphocytes	20.5 „
Mast cells	1 „

¹ Tallqvist's scale was used because it is easily carried in the pocket, and can be used for rapid work.

The blood of this fowl chick¹ contained basophile spindle-shaped cells (Pl. XLV., Fig. 18).

(δ) *Helminthiasis* is common in Grouse. The various worms found in Grouse have been well described by Dr Shipley (*vide* chapter x. p. 207, chapter xv. p. 334 and P.Z.S., 1909) and by Dr Leiper (*vide* chapter x. p. 219). With *helminthiasis*. Grouse which would be considered perfectly healthy by keepers often contain worms. One of the causal factors of disease in adult Grouse is the larval stage of *Trichostrongylus pergracilis*. The adult *Trichostrongylus* occurs in the cæca of Grouse, and sets up inflammation therein. In the blood of three adult birds dying on the moors from "Grouse Disease," I obtained differential leucocyte counts which may be thus summarised:

Eosinophiles	23·5 to 42·0 per cent.
Polymorphonuclears	7·5 to 14·0 „
Mononuclears	6·0 to 10·0 „
Lymphocytes	44·0 to 62·5 „
Mast cell	0·5 per cent.

Contrasting these counts with those given for normal Grouse, the occurrence of eosinophilia is deduced. All three of these birds, dying of "Grouse Disease," had many *Hymenolepis microps* in their duodenum in addition to *Trichostrongylus* in the cæca.

Eosinophilia is often associated with helminthiasis in mammals. Helminthiasis in Grouse results not only in an increase in the number of eosinophile leucocytes, but also in a diminution of the number of erythrocytes in the diseased birds. Thus the number of red cells found in an adult cock Grouse dying from helminthiasis was 3,250,000 per cubic millimetre—the number of red cells for a normal cock Grouse being about one million more. The hæmoglobin value estimated by Tallqvist's scale was 60 for a Grouse suffering from helminthiasis and 80-90 for healthy adult Grouse.

In spite of the incomplete character of this investigation of the blood of the Grouse (due to the lack both of material and time at my disposal), I think that there are sufficient results contained herein to emphasise the importance of parallel investigations of the blood in connection with all animal diseases.

¹ Burnett gives the following differential leucocyte count of normal fowl's blood:—Polymorphonuclear 28·8 per cent.; eosinophiles 3·3 per cent.; large mononuclears 5·5 per cent.; lymphocytes 58 per cent.; mast cells 4·3 per cent.

References to Literature.

- ADAMI, J. G. (1907).—"Inflammation: an Introduction to the Study of Pathology," 240 pages. London: Macmillan & Co.
- BURNETT, S. H. (1908).—"The Clinical Pathology of the Blood of Domesticated Animals." 156 pages, 4 pls. Ithaca, N.Y., U.S.A.: Taylor & Carpenter. ("Blood of Fowl," Pl. 3.)
- CULLEN, E. K. (1903).—"A Morphological Study of the Blood of Certain Fishes and Birds with Special Reference to the Leucocytes of Birds." Bull. Johns Hopkins Hosp. xiv. pp. 352-356.
- DANTSCHAKOFF, W. (1908).—"Untersuchungen über die Entwicklung von Blut und Bindegewebe bei Vögeln." Archiv. f. Mikroskop. Anatomie. 73, pp. 117-181, 2 pls.
- DENYS, J. (1888).—"La structure de la moelle des os et la genèse du Sang chez les Oiseaux." La Cellule, iv. pp. 203-240, 2 pls.
- FANTHAM, H. B. (1910).—"The Morphology and Life History of *Eimeria (Coccidium) avium*: a Sporozoön causing a Fatal Disease among Young Grouse." Proc. Zool. Soc. Lond. 1910, pp. 672-691, 4 pls. *Vide* chapter xi. p. 235.
- FANTHAM, H. B. (1910).—"Observations on the Parasitic Protozoa of the Red Grouse (*Lagopus scoticus*).", Proc. Zool. Soc. Lond. 1910, pp. 692-708, 3 pls. *Vide* chapter xiv. p. 318.
- FANTHAM, H. B. (1910).—"Experimental Studies on Avian Coccidiosis." Proc. Zool. Soc. Lond. 1910, pp. 708-722, 1 pl. *Vide* chapter xi. p. 252.
- MOORE, V. A. (1895-6).—"Infectious Leukemia in Fowls." 12th & 13th Ann. Rept. Bureau Anim. Industry, U.S. Dept. Agric. p. 185.
- NEAVE, SHEFFIELD (1906).—"Second Report Wellcome Research Laboratories at Gordon College, Khartoum, pp. 194-196.
- SHIPLEY, A. E. (1909).—"The Threadworms (Nematoda) of the Red Grouse (*Lagopus scoticus*).", Proc. Zool. Soc. Lond. 1909, pp. 335-350, 8 pls. *Vide* chapter x. p. 207.
- SHIPLEY, A. E. (1909).—"The Tapeworms (Cestoda) of the Red Grouse (*Lagopus scoticus*).", Proc. Zool. Soc. Lond. 1909, pp. 351-363, 5 pls. *Vide* chapter xv. p. 334.
- WARTHIN, A. S. (1907).—"Leukemia of the Common Fowl." Journ. Infect. Diseases, iv. p. 369.

CHAPTER XIV

OBSERVATIONS ON THE PARASITIC PROTOZOA OF THE RED GROUSE (*LAGOPUS SCOTICUS*), WITH A NOTE ON THE GROUSE FLY¹

By Dr H. B. Fantham

INTRODUCTION

In the following paper are recorded observations made on the various parasitic protozoa found in Grouse examined in connection with the "Grouse Disease" Inquiry.

Intro-
duction. The observations were, by force of circumstances, limited to one season, and so the accounts of some of the parasites are consequently incomplete. The parasitic protozoön of greatest economic importance, and to which most attention had to be devoted, is *Eimeria* (*Coccidium*) *avium*, which is the pathogenic agent of a fatal disease in Grouse chicks, particularly prevalent in the spring and early summer. The morphology and life-history of *Eimeria avium*, and the results of experimental studies on Avian Coccidiosis are set forth in another part of the report.² The remaining protozoa found in Grouse may be conveniently divided into (α) parasites of the blood, (β) parasites of the alimentary tract. So far I have found seven protozoa parasitic in Grouse, exclusive of the *Coccidium* already mentioned.

(A) PARASITES FOUND IN THE BLOOD OF GROUSE.

Sporozoa—Hæmosporidia

1. *LEUCOCYTOZOÖN LOVATI* Seligmann and Sambon, 1907.

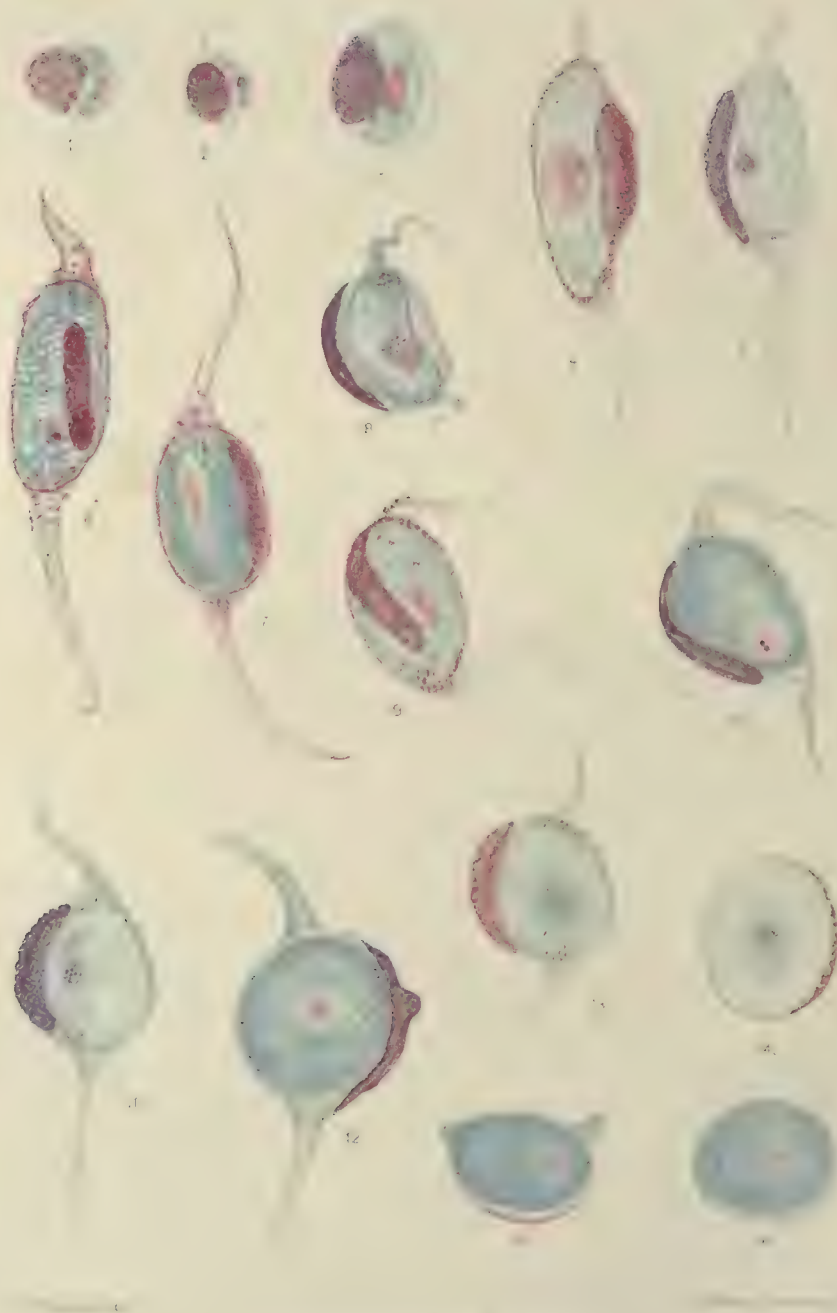
This parasite was discovered in 1907 by Seligmann and Sambon in blood-films of Grouse. It was found in one bird not suffering from "Grouse Disease." Sambon (1908-1909) refers again to the parasite, and states that he found it in five more Grouse. Sambon gives five drawings of the parasite.

Intro-
ductory.

¹ Reprinted from the *Proceedings of the Zoological Society of London*, 1910.
Vide chapter xi. pp. 235 and 252.

PLATE XLVI.

NO. 1000
ANATOMICAL



Personally, I found this parasite in 1909 in three Grouse, all of which were in splendid condition, though in one case the spleen was found to be slightly enlarged. The parasites were in no case numerous, and in one bird only the younger stages of the parasite were seen. However, in the two remaining birds I had the good fortune to find the parasites alive in both peripheral blood and in heart-blood taken from birds freshly killed. Observations were made on the living parasites, both unstained and after colouring them *intra vitam* with methylene blue (Plate XLVII., Figs. 17-22). The parasites were also seen while making blood-counts of the avian hosts, when the *Leucocytozoön* stained *intra vitam* with the methyl-violet of Toison's fluid.

The nature of the host-cell is controversial, some authorities considering that it is an erythroblast, others that it is a leucocyte, while the views of some of the observers have changed during the course of their investigations. The host-cell clearly does not contain hæmoglobin, and no melanin pigment is excreted by the parasite. The host-cell is at first round or ovoid, containing a rather broad and well-marked nucleus, and so the host-cell must be either a mononuclear leucocyte or an erythroblast. Possibly both these types of cells may be infected. The nature of the host-cell is inherently difficult to determine in view of the fact that all the blood-cells of birds are nucleated. Judging by the size of the nucleus of the host-cell (Plate XLVI., Figs. 1-3), I incline to the view that it is a small mononuclear leucocyte or potentially such. Other workers have acknowledged the resemblance of the host-cell to a mononuclear leucocyte. However, the matter can only be definitely settled by researches on the origin and development of the various blood-cells of birds—on which our present knowledge is meagre and contradictory—running parallel with the researches on infected birds, studying the young stages of the leucocytozoön.

The host-cell of *L. lovati* soon becomes drawn out at the ends, that is, the cell becomes spindle-shaped. This is probably due to a deformity of the cell brought about by the movements of the parasite within. Wenyon (1908) considers that some spindle-shaped cells occur normally in the blood of birds and reptiles. I have very rarely seen spindle-shaped cells in the blood of Grouse, though I have found spindle-shaped cells to be more numerous in the blood of fowl-chicks (*cf.* chapter xiii., Plate XLV., Fig. 18) dying from Coccidiosis. However, I would not suggest, on present evidence, that Coccidiosis is either directly or indirectly responsible for the appearance of spindle-cells in the blood.

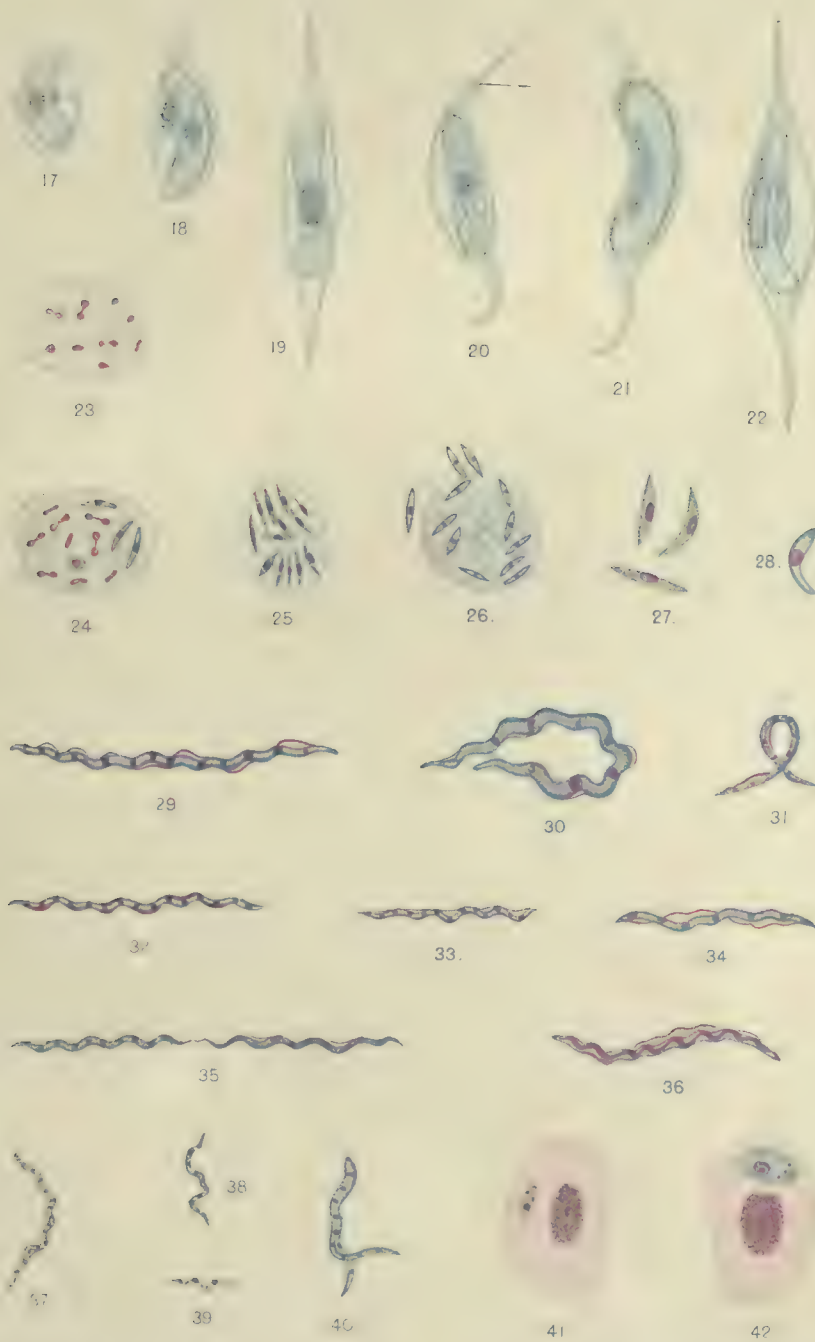
The presence of leucocytozoa does not always cause the body of the host-cell to become spindle-shaped. Mathis and Léger (1909) found that the host-cell of *Leucocytozoon caulleryi* of the Tonkin fowl did not have its ends drawn out. They also considered that the host-cell was probably a mononuclear leucocyte.

Personally, I have seen the spindle or horn-like end of the host-cell of *L. lovati* elongate during the movements of the parasite within it. Further, both ends usually are elongate (Pl. XLVII., Figs. 19-22), in other cases one end only becomes deformed (Fig. 18), while in a very few cases the cell contour has been largely unaffected by the parasite (Fig. 17). When both ends of the host-cell are affected, it not infrequently happens that the elongation of one end is greater than that of the other (Pl. XLVI., Figs. 4-6). The shape of the host-cell of different Leucocytozoa may be merely a reflex of the motility of the parasite within. It is not wise, therefore, to lay too great stress at present on the spindle-shape of the host-cells in diagnosing the Leucocytozoa of birds.

The parasite in its younger stages is vermiform and like a Hæmogregarine (Pl. XLVI., Figs. 1-3; Pl. XLVII., Figs. 17-22), and is more refractile in life than the host-cell containing it. Young forms are by no means common, a feature *L. lovati* shares with *L. caulleryi* where they have rarely been seen. The nucleus of the host-cell is displaced to one side (Pl. XLVI., Figs. 1-5), and the parasite moves very slowly within the cell, slight wave-like movements or pulsations passing from the middle of the parasite towards either end. The parasite grows in length and breadth meanwhile (Figs. 4-8), and the ends of the host-cell become gradually more and more drawn out (Figs. 4-9, and Pl. XLVII. 18-22). As mentioned above, sometimes one end of the containing cell is more drawn out than the other (Pl. XLVI., Figs. 4-6). Free vermicules of *L. lovati* have very rarely been seen in my preparations of peripheral blood.

The growing parasites gradually become round, and two forms can be distinguished to some extent in life (contrast Pl. XLVII., Figs. 20 and 22), and more easily after careful staining (Pl. XLVI., Figs. 4 and 8 from Figs. 5-7). In one the protoplasm is relatively hyaline (Figs. 4, 8, 9, 11, 13, 14); in the other form it is granular, more deeply staining, and may be slightly alveolar (Figs. 5, 7, 10, 12, 15, 16). By analogy with the malarial parasite, these rounded Leucocytozoa are considered to be gametocytes, the slightly smaller, hyaline parasites (Figs. 11, 13, 14) being characterised as males, while the slightly larger, broader, and more granular Leucocytozoa (Figs. 10, 12, 15, 16)

PLATE XLVII.



are designated females. The females or macro-gametocytes, which measure $14\frac{1}{2}\mu$ to 20μ by 10μ to 16μ , appear to be somewhat more numerous than the males or micro-gametocytes, which are about 13μ to 17μ by 6μ to 12μ . The nuclei of the gametocytes are not well marked, even after long staining. The nucleus of the micro-gametocytes (Figs. 4, 9, 13) is often somewhat larger than that of the macro-gametocyte (Figs. 6, 10, 12), is ill-defined (Figs. 11, 13, 14) in contour, and frequently has small granules of chromatin scattered within it (Figs. 11, 14). The macro-gametocyte has a better defined nucleus (Figs. 6, 10, 12), in which a larger granule of chromatin—a karyosome—is sometimes present (Figs. 5, 6, 10). Small chromatoid granules are often seen at either pole of the gametocytes (Figs. 4, 11, 13), sometimes more numerous at the ends of the micro-gametocytes (Figs. 4, 9, 11, 13) than at the ends of the macro-gametocytes (Figs. 10, 12). These chromatoid granules are, I think, more probably derivatives of the nucleus of the host-cell in process of absorption by the parasite than actual chromidia within the parasite, for sometimes the chromatoid granules are clearly outside the parasite (Figs. 6, 7).

The details of the maturation of the female gametocyte to form the macrogamete are little known—probably the macro-gametocyte becomes the macrogamete with little or no cytological change. Danilewsky (1890) and Sakharoff (1883-1885) described the formation of flagella-like microgametes from the hyaline micro-gametocyte in *fresh* preparations of the blood of certain owls, crows, and rooks. The microgametes (males) of *L. ziemannii* were considered by Schaudinn (1904) to be formed normally in the mid-gut of a mosquito which sucks the blood of the avian host (an owl). The more recent observers of avian Leucocytozoa have not usually seen gamete formation in the fresh state, so far as can be gathered from their published accounts.

Mathis and Léger (1909) have recently made the very interesting statement that there is a periodicity in the occurrence of the gametocytes of *L. caulleyri* in the blood of the fowls they investigated at Tonkin. The events of the life-cycle of the parasites in the period intervening between their appearances in the blood are unknown. There seem to me to be several alternatives possible, either the parasite undergoes a multiplicative stage in some internal organ (though it is stated that the internal organs of the fowls were examined), or a latent phase without increase in numbers of the parasite occurs, or else a re-infection of the host takes place. I have found schizogony of *L. lovati* (see p. 322) in the spleen of the host, but so far neither time nor material have been available for my observing any possible periodicity in the gametocytes of *L. lovati*, though such may occur.

Gametocytes were found to be rare in the peripheral blood, more numerous in heart-blood, and were also seen in smears of the liver and spleen of infected Grouse.

Schizogony in the avian Leucocytozoa has not been recorded before. However, in my investigations of *L. lovati*, I have succeeded in finding schizonts of this

Schizo- Leucocytozoön in the spleen of two infected birds (Pl. XLVII., Figs. 23-28).
gony.

I saw living Leucocytozoa in the heart-blood of these birds, and immediately made fresh smears of the internal organs. In the spleen were found rounded or ovoid bodies—the schizonts—with thin walls, coloured red with Giemsa's stain. These schizonts contained many merozoites (Figs. 25, 26). The capsules of the schizonts are probably formed, at least in part, by the remains of the host-cell (Fig. 26). The protoplasm of the schizonts appeared to be slightly granular (Fig. 26). Some of the schizonts already contained a few nuclei in process of multiplication by amitotic binary fissions (Figs. 23, 24), while other schizonts contained small vermicular merozoites (Figs. 25, 26) which ultimately escape from the mother cell (Fig. 26) and may be found free in spleen smears (Figs. 27, 28), when their mode of origin and general appearance are clearly grasped. A small amount of residual protoplasm is left behind in the thin membranous remains of the schizont which has just shed its merozoites. The schizonts are from 11μ to 14μ by 8μ to 11μ , and the merozoites are about 7μ in length.

The birds whose spleens contained schizonts of *L. lovati* were not infected with any other Hæmoprotozoön.

Preparations made from the bone-marrow of infected birds, in which schizogony might also take place, did not exhibit developmental forms.

The method whereby *Leucocytozoön lovati* is transferred from Grouse to Grouse has not yet been shown with certainty. The vector or second host of *L. lovati* will probably be found in some blood-sucking insect, which ingests the parasites from one Grouse and transfers them to the next bird from which it obtains blood; or perhaps there is a cycle of development of the parasite inside the Arthropod vector.

The Grouse-fly (*Ornithomyia lagopodis*) suggests itself as a likely carrier or second host of *Leucocytozoön lovati*. During my investigations I have dissected several hundreds of Grouse-flies. In the gut-contents of a very few of these flies I found unicellular motile vermicules, which may have been stages in the life-cycle of *L. lovati* or perhaps of *Hæmoproteus mansonii*. In the Grouse-flies dissected I never found cysts, such as occur in the stomachs of mosquitoes which have fed previously on blood infected with malarial parasites.

As before mentioned (p. 319), *Leucocytozoon lovati*, as it has been found to occur in Grouse on the moors, does not appear to be a serious agent of disease.

2. *HÆMOPROTEUS MANSONI* Sambon, 1908.

This parasite of the red blood corpuscles of Grouse was recorded by Sambon in 1908, but figures from originals supplied by him have only recently been published (1910) in Castellani and Chalmers' "Manual of Tropical Medicine," Fig. 55, p. 235.

In blood-films sent to me from Scotland and taken from two Grouse, I found, after staining, a few parasites inside the red blood corpuscles. Two examples of the organism are drawn in Pl. XLVII., Figs. 41-42. They appear to be young forms of the parasite, one of which showed clearly granules of melanin pigment. I regret that, owing to lack of material, I cannot give a fuller description of the organism.

It is likely that this Hæmosporidian is spread from Grouse to Grouse by the Grouse-fly, *Ornithomyia lagopodis*, in the gut of which Grouse-blood is found. In the gut-contents of the fly, unicellular vermicules apparently protozoal organisms, were sometimes seen. Further, Sambon states that "in the stomach of one [Grouse-] fly, I discovered a few hæmozoin-bearing protozoa, which were no doubt the ookinetes of the *Hæmoproteus mansonii* previously found in the blood of a Grouse from Scotland" (Sambon (1909), p. 37).

Spirochætacea (Proflagellata).

SPIROCHÆTA LAGOPODIS, sp. n.

When examining the blood of Grouse for parasites, I have occasionally found a few small Spirochætes exhibiting considerable morphological variation (Pl. XLVII., Figs. 29-40). As a Spirochæte has not been previously recorded from the blood of Grouse, I have named it *Spirochæta lagopodis*. The Spirochætes were present in blood from the heart, liver, and spleen of three birds, but were somewhat rare in each case. On one occasion I saw the parasites in life; the remaining preparations were fixed and coloured with Giemsa's stain.

Dr Sambon (1909) has noted the presence of an unnamed Spirochæte "in smears from the pulp of young feathers, and not in the general circulation" of Grouse. It is possible that *Spirochæta lagopodis* and the parasite of feather-pulp may be identical, but as details of the latter parasite are lacking, I cannot establish the

identity or otherwise. Dr Sambon also thinks that lice might act as "alternative hosts" for the Spirochætes. I will return to the subject of transmission later.

S. lagopodis is from 10μ to 18μ long, and is relatively broad for this class of organism. In life it moves actively in the blood of the host, spirally boring its way between the corpuscles. *S. lagopodis* also often entwines one part of its body about the other (Fig. 31). The organism usually has tapering ends (Figs. 29-40).

Though the Spirochæte is small, stained specimens show a fair amount of structural detail. A narrow undulating membrane (Figs. 29-36) is present, and passes spirally round the body. The thickened border of the membrane stains bright red with Giemsa's stain (Figs. 29-34), and even when the membrane is closely contracted round the body of the Spirochæte, the border can be distinguished as a bright line (Figs. 30, 32).

The chromatin of the Spirochæte is distributed in the form of bars throughout the body (Figs. 29-35), and at times these chromatin bars become joined and form a helicoid core (Fig. 36) traversing the entire length of the body. This latter condition is comparatively rare. A basal granule is present at either end, and near these granules the membrane is attached. Longitudinal division is usually initiated by fission of the basal granules.

Multiplication of *S. lagopodis* takes place by both longitudinal and transverse division. In longitudinal division rather thick Spirochætes divide (Fig. 40), the split extending gradually from one end, and the daughter forms diverging more and more until final separation occurs. Transverse division takes place in relatively long organisms (Fig. 35), and two daughter forms are produced. The parent organism elongates somewhat during the division. Very minute forms (Fig. 39) about 4μ long are the product of repeated divisions in both directions. Small forms have been seen in the spleen (Figs. 38, 39). By reference to growth following division, all the variations in size and form exhibited by *S. lagopodis* may be explained.

Regarding the mode of transmission of *S. lagopodis*, it seems to me that the nymphs of *Ixodes ricinus*, that sometimes infest Grouse, may be the carriers of the Spirochætes, for in the gut of nymphs of *Ixodes ricinus* taken from Grouse, I have found Spirochætes which may be *S. lagopodis*. During my investigations, I have dissected many Mallophaga, both *Nirmus cameratus* and *Goniodes tetraonis*, but have not found Spirochætes, though the sperm of these lice are deceptively like Spirochætes at first sight. Dr Sambon has suggested that lice act as transmitters of the Spirochæte that he found in feather-pulp. This is possible, and as a matter of fact, evidence is accumulating and tending to show that the carrying of disease

in a particular host is not restricted to any one species of Arthropod, but that several organisms, differing in genera as well as in species, may become active agents in the dissemination of protozoal parasites.

Among Spirochætes known from the blood of various birds may be mentioned *Spirochæta gallinarum* of fowls, *S. anserina* of geese, and a Spirochæte cultivated by Töpfer from the blood of the owl.

S. gallinarum is the pathogenic agent of a fatal disease in fowls, and is spread from bird to bird by the tick, *Argas persicus*.

S. lagopodis is much too rare, I think, to be a serious cause of disease in Grouse, although leucocytosis was found in a Grouse infected with *S. lagopodis*, in the blood of which bird many vacuolated mononuclear leucocytes occurred.

(B) PARASITES FOUND IN THE ALIMENTARY TRACT OF GROUSE.

(a) Flagellata.

TRICHOMONAS EBERTHI.

While examining, on the moors, the cæcal contents of Grouse—more especially for Spirochætes—I have sometimes observed a flagellate Protozoön moving therein.

The parasite was seen to possess an undulating membrane, the vibrations of which often regulated the parasite's active movements; at other times flagella were seen anteriorly whose active forward movements dragged the body of the organism onwards.

The structure of the parasite is complex. The organism closely resembles, both in size and shape, the parasite described recently (1909) by Martin and Robertson from the cæca of the fowl. The flagellate of the fowl, first seen by Eberth in 1862, was named *Trypanosoma eberthi* by Kent (1881), *Spirochæta eberthi* by Lühe (1906), while Stein, Leuckart, and Laveran and Mesnil more correctly considered it to be a *Trichomonas*. The nomenclature of the parasite is discussed at length by Martin and Robertson (1909). These authors describe both *Trichomonas* and *Monocercomonas* forms as well as a *Trypanosoma*, and state that they "have observed some cases of which the most natural explanation would be to regard the A [*Trypanosoma*], B [*Trichomonas*], and C [*Monocercomonas*] conditions as stages in one life-cycle"; otherwise the parasites are distinct and there is a mixed infection.

It seems to me that the flagellate which I have seen in the cæca of Grouse is

best named *Trichomonas eberthi*, though Eberth's original figures published in 1862 do not especially suggest a typical *Trichomonas*. However, the somewhat peculiar shapes figured by Eberth are perhaps due to the fact that the organism is very easily deformed.

In Grouse both typical *Trichomonas* (Pl. XLVIII., Figs. 43-46) and *Monocercomonas* (Fig. 48) forms were seen in life as well as in fixed and stained preparations (fixed wet with osmic acid and stained with Delafield's hæmatoxylin or Giemsa's stain). The bodies of the parasites vary from 8μ to 13μ by 6μ to 9μ .

Trichomonas eberthi possesses three flagella disposed around a slight cytostomic depression (Figs. 43-45), and arising inside the body close to a chromatin granule, the blepharoplast or kinetonucleus. The flagella are often much entangled. There is an undulating membrane with a flagellar border and short free flagellum; the membrane possesses also a chromatic base line on the body as seen in some specimens (Fig. 45). There is also a skeletal organella arising at or close to the blepharoplast and running backwards to the posterior (non-flagellar) end of the body, where it may project a little (Figs. 43-45). This stiff skeletal rod—which stains blue with Giemsa's stain—is the axostyle. A row of granules or blocks may be seen alongside the axostyle and base line of the membrane—better marked in some specimens than in others (Figs. 43-45). The nucleus is situated rather nearer the flagellar end of the body close beneath the blepharoplast, and is fairly large and more or less spherical. Chromatin granules are seen within it during the resting state, and a nuclear membrane is present (Figs. 43-46).

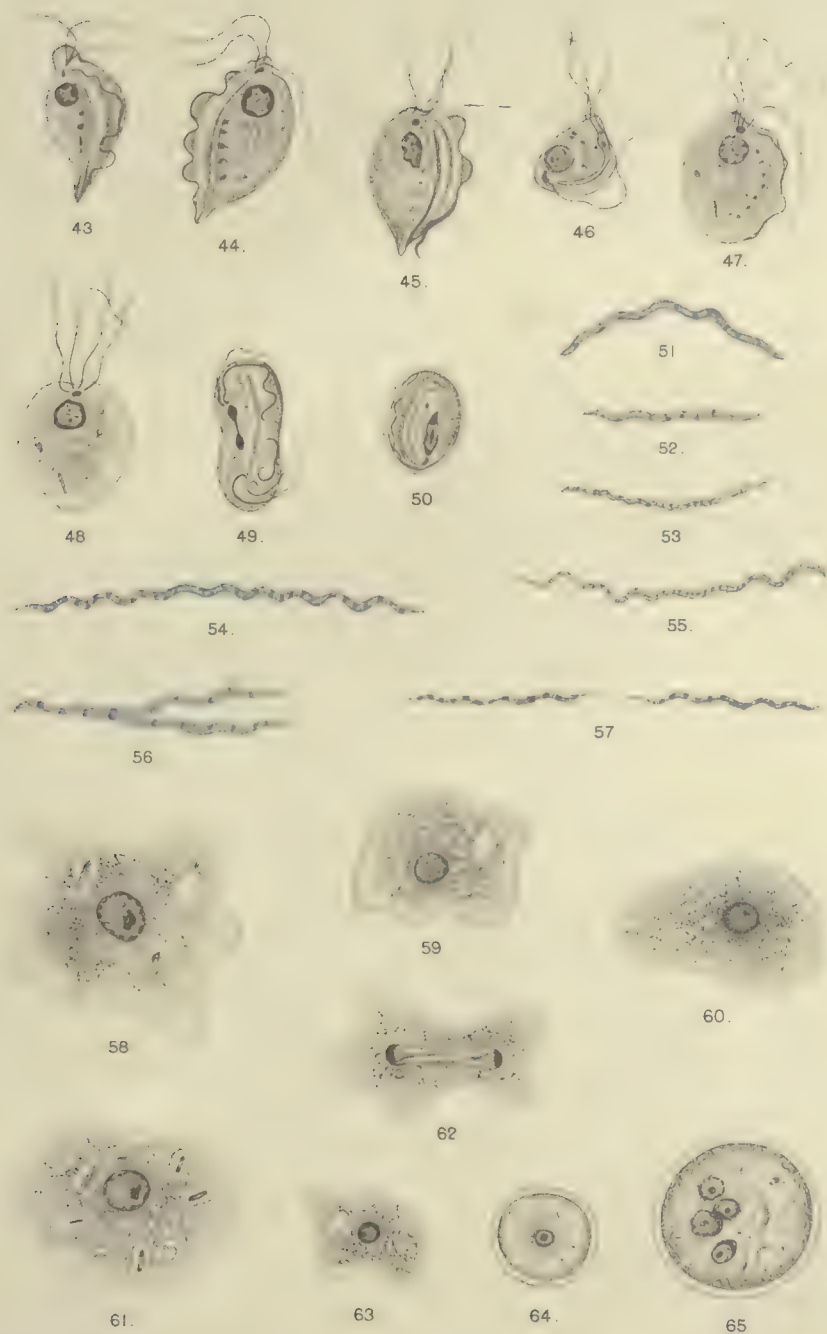
Trichomonas eberthi divides longitudinally. Although I have carefully searched for dividing forms, I have only seen them on two occasions, and then in stained preparations. One of the dividing forms is shown in Fig. 49, but I had not sufficient material to follow the details of division. The process of division is well described by Dobell (1909) for *Trichomonas batrachorum*, and by Wenyon (1907) for *T. intestinalis* in the mouse.

Encystment¹ of *T. eberthi* occurs (Fig. 50). The organism gradually becomes oval in outline, and its body substance concentrates after gradual absorption of the flagella, undulating membrane and axostyle (Fig. 50). A thin gelatinous cyst is seen in the specimen drawn (Fig. 50). Round, contracted, unencysted forms were also seen; these are probably resting forms.

Non-flagellate, irregular, immobile forms with nucleus and axostyle are occasionally seen. Amœboid forms are, I believe, the result of degeneration.

¹ B. Parisi has recently noted encystment in Trichomonads ("Arch. f. Protistenkunde," xix. p. 232).

PLATE XLVIII.



H. B. FARRAR, del.

E. Wilson, Cambridge

43-50 TRICHOMONAS EBERTHI. 51-57 SPIROCHAETA LOVATI.
58-65 AMOEBA LAGOPODIS.

Sometimes, in stained smears of the caecal contents of Grouse containing *Trichomonas*, I have seen curious ovoid or figure-of-8 bodies which suggest much deformed specimens of *Trichomonas* in which the axostyle acts as a rod around which the flagellar border and strands of the membrane are disposed. Some of these bodies are not unlike Eberth's original figures (1862).

Monocercomonas is an ovoid organism possessing four flagella at the broad anterior end of the body (Fig. 48) together with a nucleus and blepharoplast. Sometimes one of the flagella trails backward (Fig. 47). On one occasion a *Monocercomonas* form with a suggestion of a rudimentary membrane, axostyle, and granules was seen (Fig. 47). If such a parasite be normal and not deformed, then it would be an intermediate form between *Trichomonas* and *Monocercomonas* (cf. Martin and Robertson, Fig. 8).

(b) **Spirochætacea (Proflagellata).**

SPIROCHÆTA LOVATI, sp. n.

When fresh caecal contents of certain Grouse of various ages were examined microscopically, small active organisms have been seen, moving among the food débris and flora found in the gut. These organisms are Spirochætes, and their presence in the caecal contents of Grouse has also been noticed by Dr Cobbett in adult Grouse, and by Dr Leiper in a young Grouse chick. I have sometimes observed the Spirochætes in the hinder part of the intestine as well as in the caeca.

Having had the opportunity of observing this Spirochæte, which I have named *Spirochæta lovati*, I append a few details regarding its life-history and structure. I may say that the parasite does not appear to have a very deleterious effect on its host.

The organism, as observed in life, occurs in caecal contents, where it is mingled with semi-fluid food materials, and is often in company with many minute, rod-like bacteria, both free and in colonies, and also small hyphal threads, evidently of some fungus. Because of its associations, the Spirochæte is by no means easy of observation, and much dilution of the caecal contents to facilitate observation only hastens the death of the Spirochæte. Further in fixed and stained preparations the Spirochæte itself takes up the stain somewhat faintly.

The movements of the Spirochæte are active, and resemble those of the Spirochætes of Lamellibranchs (oysters, fresh-water mussels, *Tapes*) which I have already described (1907, 1908, 1909). "The motion appears to be resolvable into

at least two components: (i.) An undulatory flexion of the body, mainly for progression, and (ii.) a spiral or corkscrew movement of the body as a whole, due to the winding of the membrane." *S. lovati* has a small, but distinct undulating membrane best seen in stained preparations (Pl. XLVIII., Figs. 51-57). The ends of the organism are pointed, the length of the body being from 16.5μ to 32.5μ .

In some very narrow forms the relatively long body may be thrown into many waves (Fig. 53), but usually four to seven waves occur along the body (Figs. 51, 52, 55). The membrane with its chromatic border is often closely contracted against the body (Figs. 53, 55). The chromatin of the Spirochæte is usually present in the form of a number of bars (Figs. 51-57), which are probably disposed on a helix as is typical for Spirochætes.

After examining many specimens of the parasite it was seen that *S. lovati* exhibits morphological variation. Thus, the ends of the body usually taper (Figs. 58-59), but occasionally are somewhat rounded (Figs. 51, 52). Also the Spirochætes are of different lengths and breadths, the results of growth and division.

Multiplication of *S. lovati* by both longitudinal and transverse division has been seen in life. The division resembles that of *S. recurrentis* and *S. duttoni*, where a periodicity in the direction of division occurs (Fantham and Porter, 1909). Broad Spirochætes (Fig. 51) have been seen to divide longitudinally (Fig. 56). Longer Spirochætes (Fig. 54) often divide transversely (Fig. 57), elongating somewhat as they do so.

The modes of multiplication and the processes of growth are of the utmost importance in elucidating the morphological variation of Spirochætes.

(c) Rhizopoda.

AMŒBA (ENTAMŒBA) LAGOPODIS, sp. n.

Living amœbæ were seen by Dr Shipley (1908-1909) in fresh fæces of Grouse. I have, on a few occasions, observed amœbæ in the recently voided fæces and in the rectum and intestine of Grouse. The living organism was examined both with and without staining *intra vitam*, and a few stained preparations were made with Delafield's hæmatoxylin after fixation with corrosive-acetic-alcohol or osmic vapour, but the whole of the material was very scanty.

In structure the amœba exhibits ectoplasm and endoplasm fairly well differentiated (Pl. XLVIII., Figs. 58-63). The amœba moved slowly by sending out pseudopodia in the manner usual to these organisms, the pseudopodia being first

chiefly composed of ectoplasm. Very few pseudopodia were sent out at any one time. There is a nearly central nucleus, often possessing a karyosome. Food vacuoles containing partially digested food particles and bacteria were seen (Fig. 61). The granular endoplasm may contain a vacuole (Figs. 58, 59).

Amœboid organisms, from the irregularity of their shape, are not easy to measure precisely. More or less rounded forms may measure 60μ in diameter (Fig. 61) with a nucleus 10μ in diameter. Other specimens of the parasite (Figs. 59, 60, 63) measure from 20μ to 40μ across, with a nucleus of 5μ to 8μ in diameter.

In preparations stained with Delafield's hæmatoxylin the nucleus was seen to be spherical (Figs. 58-61) with a nuclear membrane on which the chromatin could sometimes be clearly seen in the form of granules (Fig. 58). The whole nucleus, however, is somewhat poor in chromatin, though a karyosome may be present (Figs. 58, 60, 63) as before mentioned.

Division by binary fission was seen once in life, the process taking about thirty minutes for completion. The amœba when first noticed was already elongate, and the dividing nucleus appeared as a refractile streak across the body of the parasite. A similar dividing form (Fig. 62) was once seen in a fixed and stained preparation. The nucleus was drawn out in the form of a long spindle with a central fibre, which opens out at its extremities into cone-like expansions, perhaps composed of the remains of the fibres of the nuclear spindle. The actual ends of the dividing nucleus were composed of chromatin masses or plates (Fig. 62). The division of the cytoplasm was delayed somewhat after that of the nucleus.

Encystment was rarely seen in life, and the full details could not be followed. It was noticed sometimes that, following division, the daughter individuals proceeded to encyst after a short interval, and so formed small cysts. In fixed preparations somewhat small uninucleate cysts, about 12μ to 14μ in diameter, were seen (Fig. 64). Larger cysts containing four nuclei were also found (Fig. 65), but the cysts were not numerous. The larger cysts measured about 20μ in diameter.

I am sorry that opportunity did not arise for me to make an extended study of this parasite.

Although *Entamœba histolytica* (Schaudinn) is the pathogenic agent of a form of dysentery in man, it is not very likely that *Amœba* (*Entamœba*) *lagopodis* is the cause of such a serious disease in Grouse, but *A. lagopodis* is more like *Entamœba coli*, which is usually considered to be a well-nigh harmless parasite in the human intestine.

Amœba meleagridis (Theobald Smith, 1895), which has been associated with

the disease known as "blackhead" in turkeys,¹ is now generally considered to be a stage in the life-history of a Coccidium.

(d) Sporozoa—Gregarinda.

MONOCYSTIS sp.

Spores of a gregarine, almost certainly a species of *Monocystis*, were occasionally found in the contents of the gut of a few Grouse from the Lowlands of Scotland and the North of England. The spores present much the same features as those commonly occurring in the earthworm, and show the same pseudo-navicellar appearance. The spores seem to pass through the alimentary canal of the Grouse intact. The Grouse acquire the spores accidentally by way of their food (though earthworms are not common on many Grouse moors), and the spores have no ill effect on the birds. Probably the internal heat of the bird's body aids in the development of the sporozoites within the sporocysts, though the spores are not acted on externally by the digestive juices of the host.

Uninjured spores of gregarines have been observed by L. Pfeiffer in the alimentary tract and fæces of various birds.

APPENDIX.

NOTE ON THE GROUSE-FLY, *ORNITHOMYIA LAGOPODIS*.

The relation of the Grouse-fly, *Ornithomyia lagopodis*, to the Grouse has been to some extent a matter of conjecture. Though the Grouse-flies are often found clinging to or concealed among the feathers of the birds, the biology of the fly was uncertain, and it was not known definitely whether the flies obtained blood from the Grouse or not. Having dissected several hundreds of Grouse-flies in an endeavour to find developmental stages of some of the Protozoa infecting Grouse, and possibly parasites natural to the fly itself, I append the following notes on the insect that may be of interest.

Regarding the food of the Grouse-fly, the insect sucks the blood of the Grouse. Blood in all stages of digestion has been obtained from the gut of the fly. Nucleated red cells of Grouse blood, which show no sign of digestion, are found in the red fluid in the crops of recently fed flies taken from Grouse, while on a few occasions leucocytes also have been observed. The stomach, and particularly the

¹ Since the above was written, Drs Cole and Hadley have published a memoir on "blackhead" in turkeys in America, showing that the pathogenic agent is a Coccidium (*Eimeria avium*). See Bulletin 141 of the Rhode Island Agricultural Experiment Station.

intestine, contain blood that is semi-digested, and consists almost entirely of cell nuclei.

The blood, especially in the fore-part of the gut, has a peculiar tint, and further, retains its fluidity for a very long time. Examination of the salivary glands of the fly has shown that an anti-coagulin is secreted by them. I have tested the power of this anti-coagulin in delaying the clotting of human blood, using capillary tubes of blood and emulsion, and blowing out the contents at intervals, controls being carefully kept. Blood mixed with emulsion of the salivary glands required nine minutes for coagulation, while the controls, using salt solution, had clotted in six minutes. The intestine of the fly also has anti-coagulin in it. Another member of the *Hippoboscidae*, the sheep-keed, *Melophagus ovinus*, also secretes an anti-coagulin (Porter, 1910). The blood ingested by both flies is prevented from coagulating, and thereby is kept in a more suitable condition for digestion and absorption by the fly.

The peculiar colour of the blood in the fore-part of the fly's alimentary canal is apparently to be associated with some action of the anti-coagulin, for an emulsion of the salivary glands of the fly added to human blood caused the latter to assume the same peculiar hue as was noticed in the blood from the crop of the Grouse-fly.

A fungus also infests the Malpighian tubes of the fly. The hyphal threads of the fungus rapidly develop rounded masses of spores within sporangia. The sporangia completely fill the Malpighian tubes, the spores finally bursting out as rounded bodies into the lumen of the gut, and thence pass outside the host. *Melophagus ovinus* contains a similar fungus (see Porter, 1910).

In connection with the fungus, which is common in the Grouse-flies, I may say that I have never found flagellates present where the fungus existed, and a similar condition obtains in the sheep-keed *Melophagus ovinus*.

The Grouse-fly examined as a possible vector of the protozoal parasites of the Grouse yielded rather poor results. However, I have found protozoal vermicules, some without melanin, others doubtfully with a little, in the gut of the fly. These might be stages (oökinetes?) in the life-history of *Leucocytozoon lovati* or *Hæmoproteus masoni*, or of both. There is also the possibility of *Ornithomyia lagopodis* being the transmitter of *Spirochæta lagopodis*, though I am inclined to suspect *Ixodes ricinus* here, but the whole question of the transmission of the protozoal parasites of Grouse is one demanding much more material and very careful investigation.

I also kept a number of the pupæ of the Grouse-fly for further investigation, but

unfortunately they have not hatched out yet. Dr Shipley has published an account of the Grouse-fly in which the possible time needed for hatching is discussed, together with much information regarding the adult fly (*vide* chapter xvi. p. 358).

References to Literature.

- BALFOUR, A. (1908).—Third Report Wellcome Research Labs., Khartoum. "Spirochætosis of Sudanese Fowls," p. 38.
- BLANCHARD, R. (1906).—"Spirilles, Spirochètes et autres micro-organismes à corps spirales." *Semaine méd.*, Paris, pp. 1-5.
- DANILEWSKY, V. (1890).—"Développement des parasites malariques dans les leucocytes des oiseaux (Leucocytozoaires)." *Ann. Inst. Pasteur*, iv. pp. 427-431.
- DOBELL, C. C. (1909).—"Researches on the Intestinal Protozoa of Frogs and Toads." *Quart. Journ. Microsc. Sci.* liii. pp. 201-277, 4 pls.
- DOFLEIN, F. (1907).—"Studien zur Naturgeschichte der Protozoen. V. Amöbenstudien (*A. vespertilio*)." *Arch. f. Protistenkunde*, Suppl.-Bd. i. pp. 250-293, 3 pls.
- DUTTON, J. E., TODD, J. L., and TOBEY, E. N. (1907).—"Concerning certain Parasitic Protozoa observed in Africa." *Ann. Trop. Med. & Parasitology* (Liverpool), i. pp. 287-366, 13 pls. ("Avian Leucocytozoa," pp. 288-297.)
- EBERTH, J. (1862).—"Ueber ein neue Infusorium im Darm verschiedener Vogel." *Zeitschr. f. Wissenschaft. Zool.* xi. p. 98.
- FANTHAM, H. B. (1908).—"Spirochæta (*Trypanosoma*) *balbianii* (Certes) and *Spirochæta anodontæ* (Keysseltz); their Movement, Structure and Affinities." *Quart. Journ. Microsc. Sci.* lii. pp. 1-73, 3 pls.
- FANTHAM, H. B. (1909).—"The Spirochætes found in the Crystalline Style of *Tapes aureus*: a Study in Morphological Variation." *Parasitology*, ii. pp. 392-408, 1 pl.
- FANTHAM, H. B., and PORTER, A. (1909).—"The Modes of Division of *Spirochæta recurrentis* and *S. duttoni* as observed in the Living Organisms." *Proc. Roy. Soc. B.* lxxxi. pp. 500-505.
- FANTHAM, H. B. (1910).—"The Morphology and Life History of *Eimeria* (*Coccidium*) *avium*: a Sporozoön causing a Fatal Disease among Young Grouse." *Proc. Zool. Soc. Lond.* 1910, pp. 672-691, 4 pls. *Vide* chapter xi. p. 235.
- FANTHAM, H. B. (1910).—"On the Occurrence of Schizogony in an Avian Leucocytozoon, *L. lovati*, Parasitic in the Red Grouse (*Lagopus scoticus*)." *Ann. Trop. Med. & Parasitology* (Liverpool), iv. pp. 255-260, 1 pl.
- KEYSSELITZ, G., and MAYER, M. (1909).—"Ueber ein Leucocytozoon bei einem ostafrikanischen Perlhuhn (*Guttera pucherani* Hartl.)." *Arch. f. Protistenkunde*, xvi. pp. 237-244, 1 pl.
- LEVADITI, C. (1904).—"Contribution à l'étude de la Spirillose des Poules." *Ann. Inst. Pasteur*, xviii. pp. 129-149, 1 pl.
- MARTIN, C. H., and ROBERTSON, M. (1909).—"Preliminary Note on *Trypanosoma eberthi* (Kent) (= *Spirochæta eberthi* Lühe) and some other Parasitic Forms from the Intestine of the Fowl." *Proc. Roy. Soc. B.* lxxxi. pp. 385-391, 1 pl.
- MATHIS, C., et LÉGER, M. (1909).—"Leucocytozoon de la Perdrix du Tonkin." *Ann. Inst. Pasteur*, xxiii. pp. 740-743, 1 pl.

- MATHIS, C., et LÉGER, M. (1909).—"Leucocytozoon de la Poule." C. R. Soc. Biol. 67, pp. 470-472.
- MATHIS, C., et LÉGER, M. (1909).—"Recherches sur le Leucocytozoon de la Poule. Periodicité des formes sexuées dans le sang." C. R. Soc. Biol. 67, pp. 688-690.
- MATHIS, C., et LÉGER, M. (1910).—"Sur un nouveau Leucocytozoon de la Poule." C. R. Soc. Biol. 68, pp. 22-24.
- MATHIS, C., et LÉGER, M. (1910).—"Leucocytozoon d'une Tourterelle (*Turtur humilis*) et d'une Sarcelle (*Querquedula crecca*) du Tonkin." C. R. Soc. Biol. 68, pp. 118-120.
- MEZINCESCU, D. (1909).—"Leucocytozoon ziemannii et Trypanosomes chez l'Épervier (*Falco nisus*)." C. R. Soc. Biol. 66, pp. 328-329.
- MINCHIN, E. A. (1903).—"Sporozoa" in Lankester's "Treatise on Zoology," pt. 1, fasc. 2.
- NEAVE, S. (1906).—"A New Hæmamoeba in the Blood of Guinea Fowl (*Numida ptilorhyncha*)." Second Rept. Wellcome Research Labs., Khartoum, pp. 200-202.
- NOVY, F. G., MACNEAL, W. J., and TORREY, H. N. (1907).—"The Trypanosomes of Mosquitoes and other Insects." Journ. Infect. Diseases, iv. pp. 223-276, 7 pls. (Quotes Töpfer, p. 259.)
- PORTER, ANNIE, (1909).—"The Leucocytozoa: Protozoal Parasites of the Colourless Corpuscles of the Blood of Vertebrates." Science Progress, No. 14, pp. 248-266.
- PORTER, ANNIE (1910).—"The Structure and Life History of *Crithidia melophagia* (Flu), an Endoparasite of the Sheep-ked, *Melophagus ovinus*." Quart. Journ. Microsc. Sci. lv. pp. 189-224, 2 pls.
- PROWAZEK, S. VON (1906).—"Morphologische und entwicklungsgeschichtliche Untersuchungen über Hühnerspirochæten." Arb. a. d. Kaiserl. Gesundheitsamte, xxiii. pp. 554-565, 2 pls.
- SAKHAROFF, N. (1893).—"Recherches sur les Hématozoaires des Oiseaux." Ann. Inst. Pasteur, vii. pp. 801-811.
- SAMBON, L. W. (1908-9).—"Remarks on the Avian Hæmoprotezoa of the genus *Leucocytozoon* Danilewsky." Journ. Trop. Med. and Hyg. xi. pp. 245-248, 325-328; xii. pp. 37-38.
- SCHAUDINN, F. (1903).—"Untersuchungen über die Fortpflanzung einiger Rhizopoden (Vorl. Mitteil.)." Arb. a. d. Kaiserl. Gesundheitsamte, xix. p. 547.
- SELIGMANN, C. G., and SAMBON, L. W. (1907).—"Preliminary Note on a Leucocytozoön found in the Blood of Red Grouse (*Lagopus scoticus*)." Lancet, p. 829 [Sept. 21, 1907].
- SHIPLEY, A. E. (1909).—"The Ectoparasites of the Red Grouse (*Lagopus scoticus*)." Proc. Zool. Soc. Lond. 1909, pp. 309-334, pls. 35-47. *Vide* chapter xvi. p. 347.
- WENYON, C. M. (1907).—"Observations on the Protozoa in the Intestine of Mice." Arch. f. Protistenkunde, Suppl.-Bd. i. pp. 169-201, 3 pls.
- WENYON, C. M. (1908).—Third Report Wellcome Research Labs., Khartoum. "Avian Leucocytozoa," pp. 157-165, 1 pl.

CHAPTER XV

THE TAPEWORMS (*CESTODA*) OF THE RED GROUSE (*LAGOPUS SCOTICUS*)¹

By Dr A. E. Shipley

CESTODA

THREE species of tapeworm live in the alimentary canal of the Grouse. The largest of these is (i.) *Davainea urogalli* (Modeer), which lives in the small intestine. We have also from time to time found it in the cæca; its presence there is probably due to *post-mortem* migrations. This is the tapeworm known to the keepers and to sportsmen generally. It is large, sometimes a foot or more in length and is occasionally seen protruding from the bird's anus and trailing through the air as the bird flies. The second and third tapeworms are inconspicuous and have hitherto escaped notice. One of them, (ii.) *Davainea cesticillus* (Molin), is small and very rare; we have only found it twice in the many hundreds of Grouse we have examined. It occurs, a few at a time, in the small intestine. The third tapeworm, (iii.) *Hymenolepis microps* (Diesing), is also inconspicuous, and so transparent when alive as to be almost invisible. It exists in hundreds in the duodenum, and probably causes a considerable amount of disease and death in the birds. It is by far the most dangerous of the three tapeworms of the Grouse.

(i.) Fam. *Tæniidæ*.

Genus *DAVAINEA* R. Bl. & Raill., 1891.

(i.) *DAVAINEA UROGALLI* (Modeer), 1790.

Synonyms: *Tænia urogalli* Modeer, 1790.

Tænia calva Baird, 1853.

Davainea calva Shipley, 1906.

The worm was apparently named *Tænia urogalli* by Modeer² in the year 1790.

¹ Reprinted from the *Proceedings of the Zoological Society of London*, 1909.

² "Vet. Ac. Nya Handl.," p. 129, 1790.

NO. 100
AMPHILABO



DAVAINEA UROGALLI.

E. Wilson, Cambridge

I am greatly indebted to Dr O. Fuhrmann, of Neuchâtel, for pointing out that this tapeworm is identical with that described in 1853 by Baird, and called by him *Tænia calva*.

The following is Baird's¹ description :—

"*Tænia calva* Baird, Cat. Entoz. Brit. Mus. 83.

"Head small, rounded and smooth, white and shining. Mouth unarmed. Neck constricted. Articulations of body at first very small, gradually enlarging in breadth as they descend till they reach about the middle of the body, where they are still narrow, linear-shaped, and about seven times broader than long. After this they begin to increase in length and diminish in breadth, becoming at first nearly square, and at last, near the extremity, nearly twice as long as broad. All the articulations are strongly striated across, and the upper and lower margins, where they join with each other, are considerably thickened. Length $5\frac{1}{2}$ inches, greatest breadth $3\frac{1}{2}$ lines, breadth of lower extremity 1 millimetre, of head $\frac{1}{8}$ mm.

"*Hab.* Intestines of the common Grouse *Lagopus scoticus*, Brit. Mus."

The same worm has been more fully described, also under the name *T. calva*, by F. S. Monticelli.²

The genus *Tænia* has been comparatively lately broken up into a number of other genera, and one genus, *Davainea*, named after the celebrated French helminthologist Davaine, has been established for those worms which have the rostellum and suckers armed with a multitude of characteristically shaped hooks or thorns. The genus was made in 1891 by R. Blanchard and A. Railliet, and it comprises a number of species which, as a rule, live in the small intestine of birds.

Specimens of *Davainea urogalli* vary greatly in appearance and in size. On the whole, they have in life rather an untidy, dishevelled appearance, without clear-cut features; some preserved specimens, however, had very definite outlines. Doubtless much depended on the preservative (Pl. XLIX.).

Our longest specimens measured 35 cm. in length; the greatest breadth was 4 mm. The preserved material evidently died in very varying states of contraction, and it is difficult to make general statements as to the relative proportions of different parts of the body. One specimen 35 cm. in length we found in a bird of not more than three weeks old. It was shedding ripe proglottides. This worm had split and presented a forked tail, one limb of which, however, seemed to have dwindled and come to nothing.

The head is very small. Baird gives its breadth as " $\frac{1}{8}$ mm." I should put it

¹ *Proc. Zool. Soc. Lond.*, xxi. p. 24, 1853.

² "*Boll. Soc. Napoli*," Ser. I. v. p. 155, 1891.

at about the same, but here, as elsewhere, no two specimens are exactly alike. The proglottides which follow are extremely narrow from behind forward, but they very rapidly increase in breadth, so that 6 or 7 mm. from the head the breadth is 1 mm., and at about 12 to 15 mm. it is 2 mm. The greatest breadth is usually about 2.5 mm. to 3 mm., but in some specimens 4 mm. is reached (Pl. L., Fig. 2). The broadest portion is usually about the third quarter of the body from the head; even here the segments still have but a very shallow antero-posterior diameter, about 0.6 mm. to 1 mm. Behind this region the segments narrow again. They become as long as they are broad, and but for the prominent posterior lip the segments would be square. The posterior segments are, however, longer than they are broad, and quite at the hinder end they are attached to one another by but a slender connection. The prominent posterior angle is maintained to the last (*vide* Pl. L., Fig. 2). It is, however, difficult to give precise statements as to the condition of this worm. In some, one region of the body will be swollen out; in other specimens, other regions will expand. Some have a thin, papery consistence; others are plump and almost circular in section. Sometimes the posterior rim overlaps the anterior region of the succeeding segment, so that the whole resembles the pile of conical caps which clowns used—I do not know whether they still do so—to wear in the circus. These varying conditions doubtless depend largely on the state of the parasites when killed, and on the means taken to kill them. The genital pore is, except in rare cases, on one and the same side.

The anterior end tapers quickly to the very small, squarish head. Anteriorly, the head ends in a rostellum, which seems nearly always to be retracted into a shallow recess. At each of its four corners the head bears a large sucker, as a rule circular, but at times oval in shape, and then the long axis is longitudinal (Pl. LI., Fig. 1).

Both rostellum and suckers bear hooks, which differ, however, both in their arrangement and shape. The hooks of the rostellum are arranged in a double row. Each is shaped something between a Y and a T, one arm being more curved than the other, and it is this arm which is anterior. The stalk of the hook is but very slightly curved, and the posterior row alternates with the anterior. The length of the hooks is between 6.9μ and 6.6μ . The shape of the hooks does not vary appreciably, and the arrangement in two rings is very regular. These hooks were not seen by Baird, and were first recognised in 1891¹ (Pl. LI., Fig. 3).

The hooks on the suckers are also very minute, and they vary considerably in

¹ F. S. Monticelli, "Boll. Soc. Napoli," Ser. I. v. p. 155, 1891.

PLATE L.
CONTAINS
FIGS. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100.



1. *Hymenolepis microcephala* (Urocauli) and 2. *Hymenolepis microcephala* (Urocauli) and 3. *Hymenolepis microcephala* (Urocauli) and 4. *Hymenolepis microcephala* (Urocauli)

PLATE LI.



FIG. 1. Head of *D. urogalli*. Highly magnified, with the proboscis completely retracted. This specimen shows the cal-careous bodies well, and the hooks on both the proboscis and around the suckers.

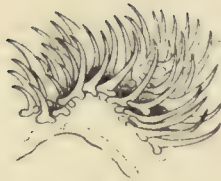


FIG. 2. Portion of the ring of hooks which surrounds one of the suckers of *D. urogalli*, showing the irregular arrangement of the hooks. Very highly magnified.

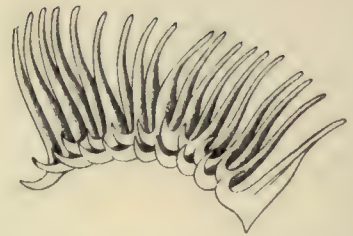


FIG. 3. Portion of the double circle of hooks from the proboscis of *D. urogalli*. Very highly magnified.

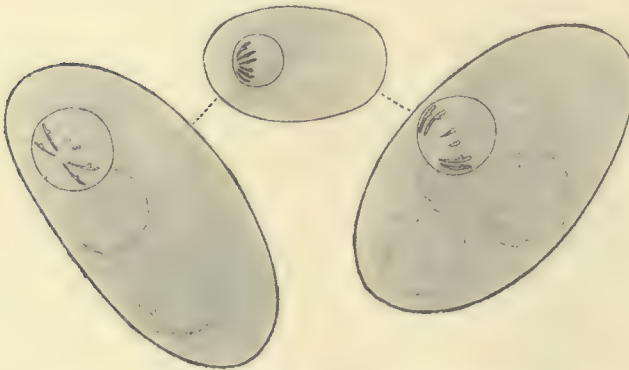


FIG. 4. Ova of *D. urogalli*. Very highly magnified, showing the six-hooked embryo or onchosphere and traces of the yolk-vesicles.

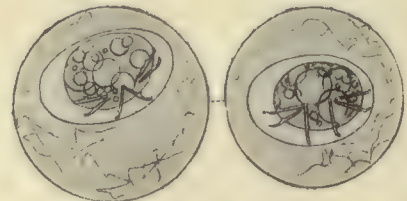


FIG. 7. Eggs of *H. microps* (Diesing), highly magnified, containing each a six-hooked embryo or onchosphere.



FIG. 6. Isolated hooks of the head of *Hymenolepis microps* (Diesing) seen under oil-immersion lens.

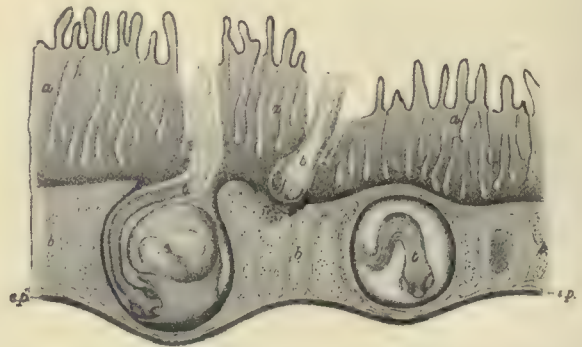


FIG. 5. Transverse section of the walls of intestine of a fowl, highly magnified, showing *Taenia botriopliti* embedded in the deep layers of the intestinal wall. *aa*. intestinal mucosa; *b*. muscular layers; *sp*. peritoneal lining; *tt*. anterior ends of the tapeworms; *e*. mass of exudate produced by the irritation of the head of the *Taenia*. (From Piana, *Mem. Ac. Sci. Instit. Bologna*, series 4, vol. ii, 1880, p. 387.)

DAVAINEA UROGALLI, HYMENOLEPIS MICROPS, ETC.

size: the largest forms are about as long as the rostellar hooks, *i.e.*, 6.6μ ; the smallest forms are perhaps half this size, and there are intermediate sizes. Each hook is slightly curved and tapers to a fine point, each possesses a "heel" which, as is shown in Pl. LI., Fig. 2, is developed in a varying degree. In many cases the proximal end resembles the "head" of a thigh-bone. The hooks are arranged in a ring, but the ring contains no definite and regularly arranged rows, rather it is a small circular forest or hedge of hooks of varying sizes and shape.

The head is usually followed by an unsegmented neck, three or four millimetres in length, but I have seen one or two specimens in which the segmentation occurs immediately behind the head. In transparent specimens longitudinal muscles running to the suckers can be seen traversing the neck. In most specimens the reproductive pore is on one side of the body throughout its entire length, but in others, more rare, it changes over, and having been for the anterior half of the body on the right side it suddenly passes to the left and remains there till the end.

The number of the proglottides varies with the length of the worm. An average-sized specimen would have between two hundred and fifty and four hundred proglottides; each of these might contain, say, a couple of hundred eggs. These figures, though necessarily rough, give some idea of the number of ova a single tapeworm may contain at any one moment. But mature proglottides are always breaking away, and fresh ones are always being formed, like the ciphers of a recurring decimal, so that the number of ova a tapeworm produces in the course of its life is very much greater than the number it contains at any one moment.

Although the male and female reproductive openings are close together, the male orifice is very clearly anterior to that of the female. It leads into a muscular protrusible penis, which was in all cases retracted. The penis ends in a much coiled vas deferens, which runs slightly obliquely half across the proglottis, near to the anterior edge; here it ends in a number of diverticula which form the testes. These are scattered throughout the parenchyma. The wall of the vas deferens is thin, its lumen is spacious, and it acts as a vesicula seminalis. The lumen is lined by a thin cuticle, and outside this and all around it are a number of spherical or oval cells which, without exactly forming an epithelium, probably secrete the cuticle.

The vagina opens immediately behind the vas deferens. Its outermost part is thick-walled, and the lumen contains some homogeneous substance which stains deeply; further on the wall becomes thinner, the lumen more capacious, and here masses of spermatozoa are to be seen. The ovaries are two, right and left, each

rather of a cauliflower shape; they contain rounded ova in which besides the nucleus a second deeply staining body is sometimes seen. The vagina makes a turn through about a right angle, and passing between the two ovaries, where it receives the two oviducts, it travels back to the vitellarium, a somewhat pyramidal body lying close to the posterior end of each proglottis. Certain unicellular glands in this region of the female duct are probably shell-glands.

There seems to be no walled uterus, but the fertilised ova are scattered throughout the body embedded in the parenchyma. Each is a large oval cell with very vacuolated protoplasm and a nucleus at one side and numerous yolk-granules.

Monticelli describes the proglottides as longitudinally striated, and the striations as due to the longitudinal muscles. These are certainly conspicuous in section, although in our specimens the external striation was not very well marked.

One striking feature of *D. urogalli* is the great extent to which the water vascular system is developed. It is spacious and large in the anterior segments, but in the posterior half of the body it becomes very much larger. The lumen of the lateral canals increases, and the transverse duct which unites them at the posterior end of each proglottis swells out amazingly. From being a slender duct it enlarges to a great spherical chamber, of which the sides, which will rupture when the proglottis drops off, are extremely thin.

When the ova are squeezed out of a living ripe proglottis of *D. urogalli*, they present the appearance shown in Pl. LI., Fig. 4. Each egg contains a six-hooked embryo which is much smaller than the egg-shell. Besides the six-hooked embryo, the egg-shell contains two or three spherical bodies usually of about the same diameter as the embryo, but sometimes smaller. These are apparently yoke-spheres in course of absorption; the remainder of the egg-shell is empty. The shape is similar to that of the hooks figured in the sketches of *Davainea* embryos in Blanchard's article¹ (Pl. LI., Fig. 4).

The genus *Davainea* occurs in many birds, Cursores, Gallinaceæ, Columbinae, etc., and much more rarely, in the form of *Davainea madagascariensis* (Dav.), in the intestine of man. Little is known of their second hosts; they are usually believed to be insect larvæ, centipedes or land molluscs. Grassi and Rovelli² consider the intermediate host of the *D. proglottina* of the common fowl to be *Limax cinereus*, *L. agrestis*, and *L. variegatus*. In this case the cysticeroid is fully developed in the slug within twenty days. If the slug be swallowed by a fowl the

¹ "Mém. Soc. Zool. France," iv. p. 420, 1891.

² "Centrbl. Bakter.," iii. p. 172, 1888.

cysticeroid becomes adult at the end of eight days. We have sought for the cystic form in *Limax flavus* without success.

Davainea echinohothrida,¹ which is possibly a synonym of *D. tetragona*, causes a nodular disease in poultry,² a condition liable to be mistaken for tuberculosis. This disease was first recorded in the United States by Moore (1895),³ from whose article the following extracts are made:—

“The nodules were invariably more numerous in the lowest third of the small intestine. They occasionally appeared, however, in small numbers in both the duodenum and colon. The larger and to all appearances older nodules were found in the ileum near the cæca.

“In the badly affected portion the nodules gave the appearance of closely set protuberances, varying in size from barely perceptible areas of elevation to bodies 4 mm. ($\frac{1}{8}$ inch) in diameter. In some instances they appeared to overlap one another. When separated by a band of normal tissue they were round or somewhat lenticular in form. In the latter case the long diameter was usually transverse to the long axis of the intestine. The larger nodules were of a pale dark-yellowish colour, while the smaller ones varied in shade from the more highly coloured areas to the neutral grey of the normal serosa. To the touch they gave the sensation that would be expected if the subserous and muscular coats were closely studded with small, oval, solid bodies. The mucosa presented similar elevations. Attached to the mucosa over the nodules were a number of tapeworms. There were also in the more advanced cases a variable number of small (0.5 to 1 mm.) areas over the larger nodules in which the mucosa had sloughed, leaving small ulcerated depressions.

“The larger nodules contained a greenish-yellow necrotic substance, which appeared in the advanced stages as a sequestrum with a roughened surface. On section it has a glistening, homogeneous appearance. Surrounding the necrotic substance was a thin layer of infiltrated tissue. The smaller nodules contained a more purulent-like substance, and the smallest appeared to the naked eye as areas of infiltration. Sections of the affected intestine showed upon microscopic examination that the heads of the tapeworms had penetrated the mucous membrane, and were situated in different layers of the intestinal wall (*cf.* Pl. LI., Fig. 5). They were frequently observed between villi. As would be

¹ B. H. Ranson, “Manson's Eye Worm of Chicken, etc.,” Bureau of Animal Industry, U.S.A., Bulletin 60, 1904.

² D. E. Salmon, “Tapeworms of Poultry,” Bureau of Animal Industry, U.S.A., Bulletin 12, 1896.

³ V. A. Moore, Bureau of Animal Industry, U.S.A., Circular III., 1895.

expected, the heads were not readily detected in the necrotic masses contained in the larger nodules, but were almost invariably seen in the smaller ones. In a few sections the tapeworm could be traced through the mucosa to the nodule in the muscular tissue in which its head appeared. In the earlier stage of the nodular development there is a cell infiltration about the head of the worm. This process continues until the infiltrated tissue reaches a considerable size.

"The worms attached to the mucosa were usually small. A larger form was commonly found in the intestinal contents. Although microscopically they appeared to be different, Doctor Stiles found that they were presumably of the same species.

"*Economic Importance.* — The importance of this disease is much greater than it at first appears, as the close resemblance of the nodules to those of tuberculosis renders it of much significance from the differential standpoint. As the intestines are stated to be frequently the seat of the specific lesions of tuberculosis in fowls, it is of the greatest importance that a thorough examination be made before a positive diagnosis is pronounced. There are already several statements concerning the presence of tuberculosis in fowls in which the data given are not sufficient to differentiate the disease from the one here described. A somewhat analogous disease of sheep caused by a nematode (*Esophagostoma columbianum* Curtice) has led to the deliberate destruction of many animals, the owners believing that tuberculosis was being eliminated from their flocks.

"As the inquiry into the cause of poultry diseases becomes more general it is probable that this affection will be occasionally encountered, and unless its nature is recognised it may in some instances, like the sheep disease, lead to an unwarranted destruction of property.

"In addition to its importance in differentiating tuberculosis it is in itself a malady worthy of careful attention. The fact that it has already appeared in two flocks in the District of Columbia, and also in the States of North Carolina and Virginia, shows that the infesting cestode is quite widely distributed in this country. It is highly probable that the total loss it occasions, both from deaths and from the shrinkage of poultry products, due to the chronic course of the disease it produces, is very large."

(ii.) *DAVAINEA CESTICILLUS* (Molin), 1858.Synonym : *Tania cesticillus* (Molin).

This is a small species ; the majority of our specimens measured between 5·5 and 9 mm. in length. Few were longer, though many were shorter. They were all young immature specimens. The broadest at the broadest part, usually about the level of the last proglottis but two or three, measured 1 mm. across. They tapered to the last proglottis, which averaged about 0·5 mm. in diameter, and still more do they taper towards the head, where the narrow neck is but 0·2 mm. The head itself is 0·3 to 0·5 mm. across, and perhaps two-thirds of this in length.

The hooks in the rostellum were numerous, I should judge a few hundred, but I could not, on account of their minute size, count accurately : they measured about 7μ in length.

The head when the rostellum is withdrawn is somewhat cup-shaped, and the four suckers are on the edge of the cup, opening at the edge and slightly inwards. There is practically no "neck," just a constriction between the head and the first proglottis. Behind the head the proglottides increase markedly in size, and the third proglottis in most specimens is already as broad as the head. They are deeply imbricated, and the overlapping edge is full and rounded. At the level of the anterior end of each proglottis is a constriction which slightly separates off the overlapping lobe from the preceding proglottis, to which it, of course, belongs. This gives a somewhat ear-like outline to the side of each segment. The constriction first appears in about the tenth proglottis, and the characteristic outline is lost in the last, where the overlapping edges curve in as if to guard the excretory opening. The total number of the proglottides varies a little with the variable length, but differences in length depended far more on the state of contraction of the body than on the number of segments. Roughly speaking, the numbers varied from about eighteen to about twenty-eight proglottides.

The genital pore is alternate, and fairly regularly so ; the penis often projects, and then it is apparent that the pore lies rather anteriorly, and is all but overlapped by the imbricated edges of the proglottis next in front.

Sections show that there are a number of calcareous bodies in the tissues ; some of these are in optical section brick-shaped, and others spherical or shaped like a cottage-loaf. These latter are bigger than the others, and show numerous radiating lines. Posteriorly the tissue becomes very highly vacuolated, and the

embryos lie in small packets which do not seem to be in a uterus, and may be, as Morell suggests in *D. urogalli*, in the lumen of the ovary itself.

This tapeworm, common in chickens and turkeys, is only an occasional parasite of the Grouse, and has in many hundreds of birds we have examined only been found twice, and in neither case has its presence been associated with any lesions. As a factor in "Grouse Disease" it may be neglected. In both cases only young, immature, not fully-grown specimens were met with. Its second host is according to Railliet, quoting Grassi and Rovelli, probably some Coleopteran or Lepidopteran; but at present this has not been proved.

HYMENOLEPIS Weinland, 1858.

(iii.) HYMENOLEPIS MICRIPS (Diesing), 1850.

Synonyms: *Tenia microps* (Diesing), 1850.

Hymenolepis tetraonis (Wolffh.), 1900.¹

This is an extremely delicate transparent tapeworm which exists in almost countless numbers in the duodenum of *Lagopus scoticus*. It is also recorded from the Blackcock and the Capercaillie. On cutting open the duodenum of a Grouse infested with these worms—and we have rarely found a bird free from them except in the winter months—they are not at first apparent. They are so fine, and so transparent that they are practically invisible when alive, and the contents of this part of the alimentary canal appears very much like a thick purée. If we add to this some fixing agent such as corrosive sublimate this purée resolves itself into a mass of very fine, delicate, white threads inextricably tangled up together, and so numerous that there seems but little room left in the duodenum for the passage of the food (Pl. LII.). If, with great care—for they break at the slightest strain—we succeed in disentangling one of those worms we shall find its head embedded to a greater or less extent in the mucous lining of the duodenum, into which, to use a poetic phrase, "it nuzzles," whilst the body of the worm floats freely in the fluid contents of this part of the alimentary canal. If we also succeed in freeing the head we now have a complete worm, and can study its structure.

Before giving some of anatomical details of *H. microps* it is worth mentioning that Wolffhügel found fragments of this species—none with the head—in the small intestine, large intestine, and end—he does not say which end—of the cæca of *Tetrao urogallus*. We have also found short chains of ripe proglottides passing

¹ K. Wolffhügel, "Beitrag zur Kenntniss der Vogelhelminthen," Inaug-Diss., Freiburg-i-B., 1900.

View of
the specimen



HYMENOLEPIS MICRIPS.

F. W. M. 10000000

down the alimentary canal on their way to the exterior, but the tapeworm as an individual lives only in the duodenum.

H. microps is a very long worm, attaining in the longest examples a length of some 15-16 cms. It consists of an enormous number of proglottides. The first two millimetres which come after the head contain as many as sixty to seventy segments, and lower down the body, where the proglottides were mature, as many as ten proglottides measured but 1 mm. Of course these measurements depend entirely on the state of the contraction of the worm, but if we take the mean between them as a rough average approximation we shall get the astonishing number of three thousand proglottides in a single specimen. As each proglottis contains a large number of eggs, and as they are being continually renewed, and as, further, the number of tapeworms in the duodenum amounts to hundreds, it is easy to see that a Grouse moor must be peppered with ova.

The head is somewhat squarish, with a central retractile rostellum and four suckers at the corners. The rostellum is surrounded by a closely-packed ring of very numerous spines or hooks. These are very minute and, except in the fresh specimen, very difficult to see, even then it requires an immersion-lens to make out anything of their structure. Their proximal end is rounded, and then comes a constriction; the spine then thickens till about the middle of its length, when it tapers to a very fine point. Although these spines are slightly curved, they are in no sense hooked (Pl. LI., Fig. 6). I have tried to measure the length of these spines from specimens of the head, which has been cut in sections. I am not quite sure that the hooks were entire, and so am not quite sure that my measurement is large enough, but I should put their length at about 16μ —certainly not less. The hooks seem to be in a single row, and very close together.

The suckers are deep and well marked, but it must always be borne in mind how very small the head is, and corresponding with this the suckers are also very minute.

The posterior edge of each proglottis is "saillant," but it does not overhang the succeeding proglottis; it stands out like the tooth of a saw, and viewed laterally the side of this worm is very saw-like. Throughout the body the proglottides are much broader than they are long. In the older ones there are numerous calcareous bodies, the measurements of which Wolffhügel gives as 0.018 mm. by 0.01 mm.

The genital pore is on the same side in all the segments; the left side, judging by the orientation suggested by the female reproductive organs, being on the ventral surface. The vagina opens into a peculiarly large and muscular receptaculum

seminis, which runs across the proglottis and then turns backward; in some preparations this turn is seen "en face," and then the radiating muscles give the appearance of a ring of very fine spines, and, indeed, at first I thought that there was such a ring, but I believe the above is the true explanation. There are three testes, the vasa deferentia of which unite, and after entering the cirrus-bulb enlarge to form a vesicula seminalis. The vagina opens ventral to the penis. The uterus is a single chamber unbranched. It forms a conspicuous feature in the hinder end of stained specimens. At first it appears as a spherical organ lying in the middle line at the hinder end of each proglottis, but as it grows and absorbs more of the parenchyma it tends to become triangular or square, but always with very rounded angles. It contains a large number of relatively large onchospheres or tape-worm-embryos (Pl. LI., Fig. 7). According to Wolffhügel, the embryos measure 0.02 mm. in breadth by 0.04 mm. in length. The typical six embryonic hooks are very characteristic. The partners in each pair, for instance, are usually widely divaricated; their length is 0.014 mm. These characteristic *Hymenolepis* ova have three envelopes: the innermost, closely applied to the embryo, is never produced into horns; between it and the middle envelope is only a clear fluid in which the embryo floats; between the middle and the outer envelope are the much vacuolated remains of cells. The position of the embryo is eccentric with regard to this outer shell, which measures 0.073 mm. by 0.066 mm. The measurements are again Wolffhügel's.

We have no information about the fate of these embryos, but as a general rule the cystic form of this genus lives in some insect or myriapod, as is shown by the fact that this genus of tapeworm occurs in bats, insectivores, rodents, and insectivorous birds. *Hymenolepis nana* occurs in man, most frequently in children, and is not at all uncommon in Italy. Sporadic cases of *H. diminuta* occurring in man are also recorded.

We have made laborious investigations to try and discover this second host. In searching for the cysts of the tapeworms we began with the insects which occurred most commonly in the crop of the Grouse. These we examined microscopically, both after teasing the body up in glycerine and by grinding it up—but not too finely—in a mortar; in some cases also, as Mr Fryer¹ has recorded, sections were made and examined, but always without result.

We were at two disadvantages in hunting for the cysts: firstly, we did not

¹ Interim Report of the "Grouse Disease" Inquiry.

know what the cysts of either *Davainea urogalli* or *Hymenolepis microps* were like; and, secondly, the tissues of the insects and spiders which we examined are little, if at all, known, and more than once we have at first sight taken some organ proper to the insect for a cestode cyst, only to our great disappointment to discover later that we were looking at an ovum or other structure belonging to the putative host.

During some days Dr Wilson and I spent in Edinburgh towards the end of July 1908, we examined a considerable number of the commoner insects found on the moors in the hope of throwing some light upon the life-history of the tapeworms so common in the Grouse. The specimens we investigated were collected by Mr P. H. Grimshaw, who has prepared a Report on the Insects of the Moors. We are greatly indebted to him and to the Keeper of the Museum, Mr W. Eagle Clarke, and to Mr. J. Ritchie, for kindly placing at our disposal a workroom and other accommodation which greatly facilitated our work. When the insect had not been specifically named, we always kept a similar specimen for subsequent identification in case it should contain the cyst; but, alas! here again our labour was in vain.

In the manner indicated we examined the following insects, in every case looking through the débris of some four or five specimens.

DIPTERA.

(i.) *Monophilus ater*, one of the subfamily Limnobiinæ of the Tipulidæ. A very common constituent of the food of young Grouse. No trace of a cyst was found, but in one specimen an immature nematode was wriggling about.

(ii.) *Bibio* sp. Here again we drew a blank.

(iii.) *Cyrtoma spuria*, one of the Empidæ. This fly is small, and seemed to have little interior; no trace of a cyst was found. In another small empid fly we discovered a Gregarine.

(iv.) *Scatophaga* sp. *Scatophaga stercoraria* is perhaps the commonest fly in Scotland, and, owing to the larva living in the droppings of the Grouse, it can hardly fail to contain the eggs of the cestodes; but we have never found a *Scatophaga* in the crop of a Grouse, and there is some reason to doubt if the tapeworm eggs develop in this fly. After searching for a long time, through the tissues of many specimens of *Scatophaga*, we only managed to find one ovum apparently of *Davainea urogalli*, and that was no further advanced than when it was laid.

PLECOPTERA.

Similar gropings through the dissected membranes of an unknown species of perlid produced no better results.

ARACHNIDA.

We also investigated the tissues of a spider very common on the moors, and of a phalangid, with an equal want of success.

NOTE BY WM. BYGRAVE, M.A., ON THE SEARCH FOR CYSTS.

Since September 1908 I have been making a series of investigations in connection with the "Grouse Disease" Inquiry. My work has consisted of a careful examination of the tissues of certain insects found on Grouse moors in various parts of England and Scotland, the object being to discover, if possible, cysts of the three species of tapeworm which infest the Grouse, viz. :—

Davainea urogalli (Modeer, 1790).

Davainea cesticillus (Molin, 1858).

Hymenolepis microps (Diesing, 1850).

The insects examined to date are specimens of *Scatophaga squalida* from Ballindalloch, and *S. stercoraria* from Burley, Dunachton, and Forrigen.

The specimens were sent to me by Mr P. H. Grimshaw, from the Royal Scottish Museum, Edinburgh, preserved in spirit.

The method of examination was as follows :—

The legs and head were removed and the body of the insect teased up in 70 per cent. alcohol as finely as possible with needles, the legs and head being firstly teased and then gently pounded in a mortar.

The material thus obtained was examined under a cover-glass, a mechanical stage being used to ensure that none of the material was overlooked. The powers used were Leitz Obj. $\frac{1}{4}$ inch and $\frac{1}{8}$ inch Oc, 2 and 4 ; an oil immersion-lens being used in cases of doubt. So far the examination has yielded no results. Nothing has been found which in any way resembled the cysts, one or two of which have been figured of species allied to the three tapeworms mentioned above.

CHAPTER XVI

THE ECTOPARASITES OF THE RED GROUSE (*LAGOPUS SCOTICUS*)¹

By Dr A. E. Shipley

FIVE years ago we knew two internal parasites of the Grouse (endoparasites) and two or three parasites which live outside the skin (ectoparasites). At the present time we know that Grouse, like other animals, have a considerable Parasites of the Grouse. fauna living both in and on them. The scientific members of the Inquiry have recorded nine different species of insect or mite living either amongst the feathers or on the skin of the bird, or in other ways associated closely with the Grouse, and no fewer than fifteen animal parasites living in the alimentary canal, in the blood, in the lungs, or other organs. Some of these are negligible. They either exist in too small numbers or infest but a very small percentage of birds; others, however, are found in about 95 per cent. of the cases investigated, and two at least are associated with grave disorders which often terminate in death.

From the point of view of the "Grouse Disease" Inquiry, the attention paid to the ectoparasites may seem superfluous, but many of the internal parasites and all the tapeworms pass through a second host. For example, the tape- Importance of ecto-parasites. worms which live in the alimentary canal of the Grouse pass their younger or larval stages in the body of some lower animal. This lower animal, presumably an insect or a mollusc or a spider, must be eaten by a Grouse, and the larval tapeworm must be set free before the latter can grow up into the adult tapeworm which we find in the intestine of the Grouse. In searching for this second host it was natural to begin with the ectoparasites, which one would imagine were continually being snapped up by the bird. We have, however, up till now completely failed to find any cestode-larvæ in the Grouse-fly, or in the numerous "biting-lice" or "bird-lice" (Mallophaga) which abound on the skin and amongst the feathers of the Grouse; and, what is still more significant and still more remarkable, we have, in the hundreds of crop-contents which we have examined, never found one of these insects in the Grouse's food.

¹ Reprinted from the *Proceedings of the Zoological Society of London*, 1909, with a few alterations

This report is based in the main on my own observations, but some of the facts recorded were first observed by Dr E. A. Wilson, and some by Mr J. C. F. Fryer, of Caius College, Cambridge. In fact, in looking back over the work I find it difficult to disentangle the precise share each of us had in it. One thing, however, is clear. I am indebted to Dr Wilson for a very large proportion of the drawings which are reproduced in these chapters, and I am also indebted to him for lightening many pleasant hours spent, not on the open, breezy heather of the Scottish moors, but in the stuffy laboratory we were wont to improvise in the back premises of many a Scottish inn.

To Mr Edwin Wilson, of Cambridge, a word of thanks is also due for the accuracy and skill with which he has depicted the Grouse-fly and the Grouse-flea.

ECTOPARASITES.

INSECTA.

A. MALLOPHAGA.—Bird-lice or Biting-lice.

(i.) Fam. Philopteridæ.

I.—*GONIODES TETRAONIS* Denny.

In his "Monographia Anoplurorum Britanniae,"¹ Denny describes and figures this species, which he calls the "Louse of the Black and Red Grouse." He states that it is "common upon both the Black and Red Grouse" (*Lagopus tetrix* and *L. scoticus*). "Upon the Willow or Hazel Grouse (*Lagopus saliceti*) I find a similar but distinct species, rather broader in the abdomen, and of much darker colour." Denny describes several species of the same genus which infest other game-birds.

Giebel² gives the name *Goniodes heteroceros* Nitzsch as a synonym of *G. tetraonis*, and in his large monograph on "Les Pédiculines," Piaget³ uses the former name without any reference to Denny. The name *G. heteroceros* also appears in Giebel's article⁴ on the Epizoa of the Halle Museum, published in 1866, but only the name. In his article on "Parasiten" in Von Middendorf's "Reise in den äussersten Norden und Osten Sibiriens," Grube attributes certain bird-lice taken from *Lagopus albus*, the Willow Grouse, and from *Lagopus alpinus*, the Ptarmigan, to the species *Goniodes tetraonis* Denny; but Piaget points out certain

¹ Published by H. G. Bohn, London, 1842, p. 161, Plate xiii., Fig. 3.

² "Insecta Epizoa," Leipzig, 1874.

³ Leiden, 1880.

⁴ "Zeitschrift für gesammten Naturwissenschaft," xxviii. p. 387, 1866.

differences, and seems to consider that a new species might have been described from these specimens.

Andrew Murray, in his book on "Economic Entomology,"¹ writing of *Goniodes tetraonis*, says: "This is the insect which sometimes, especially in the bad seasons, does so much harm to the young Grouse when they are feeble and unhealthy."

It is the commonest of the insects which infest the skin of Grouse, crawling about amongst the base of the feathers and on the vane of the feathers themselves. It occurs more commonly than *Nirmus cameratus*, which is often associated with it. It is comparatively rare to find a bird free from these "biting-lice," but perhaps 10 per cent. is about a fair estimate of the number of uninfested Grouse. The number on each bird is to some extent an inverse measure of their health. Careful search will discover but two or three on a healthy Grouse, but on a "piner" hundreds may be met with. This is not, however, the case with birds that die quickly of acute disease.

Goniodes tetraonis is usually found on the smaller feathers, crawling about halfway between their insertion and the tip of their vanes. When disturbed they hurry away into the brushwood of the small feathers, like small deer seeking cover, and they are by no means so easy to catch as one would at first think. They eat the finer barbules of the feathers, which, accumulating in the crop, give the dark curved marking in their rather transparent bodies. On this meagre and arid diet they seem to flourish, actively produce young, and pass through several ecdyses.

The naked-eye colour of *Goniodes* is a yellowish brown. Under the microscope the body appears rather transparent, but wherever there is chitin this is of a yellowish to chestnut-brown colour according to the thickness. The crop, which is full of minute fragments of the finest barbules of the feathers, presents a blackish sac-like appearance, running obliquely across the middle line of the abdomen; a somewhat parallel but much smaller black tube represents possibly the rectum (Fig. 4). In a few cases the œsophagus and crop presented a red appearance, this being probably due to hæmoglobin from the blood of the Grouse. The body is, on the whole, flattened—especially is this the case with the head and abdomen. The thorax, as Snodgrass² points out in *Menopon persignatum*, appears to be triangular in cross-section.

The head is shaped somewhat like the semicircular knives used for cutting

¹ Chapman & Hall, London, 1877.

² "Occasional Papers of the California Academy of Sciences," vi. p. 145, 1899.

cheese. The head of the female is somewhat broader and shorter than that of the male, and is produced at the posterior-lateral region into a much more prominent angle. In both male and female the angle bears a spine and a long hair. The anterior margin of the head is bounded by a thick rim of chitin, beneath which is a layer of granular protoplasm with a few nuclei, the hypodermis. At intervals the chitin is pierced by narrow channels, into which the hypodermis extends, and the chitin bears at the outer end of each of these channels a short sensory hair.

There is no neck, but the first segment of the prothorax is only about one-half the width of the head. The mesonotum is fused with the metanotum, and the thorax appears to have but two segments. There is, again, no waist or constriction between the thorax and the abdomen, but the segments from the first thoracic to the second or third abdominal gradually and uniformly widen, and then as uniformly diminish in width until the last.

According to Sharp¹ the Mallophaga have from eight to nine abdominal segments, and according to Railliet² the family in which he places *Goniodes* has nine; but he remarks that the last two are sometimes completely fused, so that we only find eight visible segments.

There are certainly only eight visible in *Goniodes*, although *Nirmus* has nine complete segments. The last visible segment in the female is a slightly bilobed plate bearing no hairs; the anus opens just below it. In the male the plate is not bilobed; it is stouter, and bears a number of backwardly projecting hairs. Each segment, except the last in the female, bears a number of hairs (Pl. LIII., Figs. 1 and 2).

The appendages are as follows:—

I. *The Eyes*.—Each eye is formed of a little aggregation of pigmented cells, the whole somewhat cup-shaped, and of an almost spherical transparent thickening of the cuticle, the lens. The eyes are situated close behind the thickened cavity from which the antennæ arise.

II. *The Antennæ*.—These arise from a deep hollow, the chitinised walls of which are much thickened. The cavity practically conceals the proximal joint, which is broader than long; the second joint is the longest, and is almost twice as long as its broadest part; the third, fourth, and fifth segments uniformly diminish in size, and the fifth or last bears at its end a number of

¹ "Cambridge Natural History," vol. v. Insecta, i. London, 1895.

² "Traité de Zoologie Médicale et Agricole," 2nd edn. Paris, 1895.



FIG. 1. *Goniodes tetraonis*. Denny. Male seen from above. The legs are shown on the left side only. The forked character of the antennæ of the male and the male genital plates in the abdomen are shown.



FIG. 2. *Goniodes tetraonis*. Denny. Female seen from below. The unbranched antennæ and biting jaws are well shown.

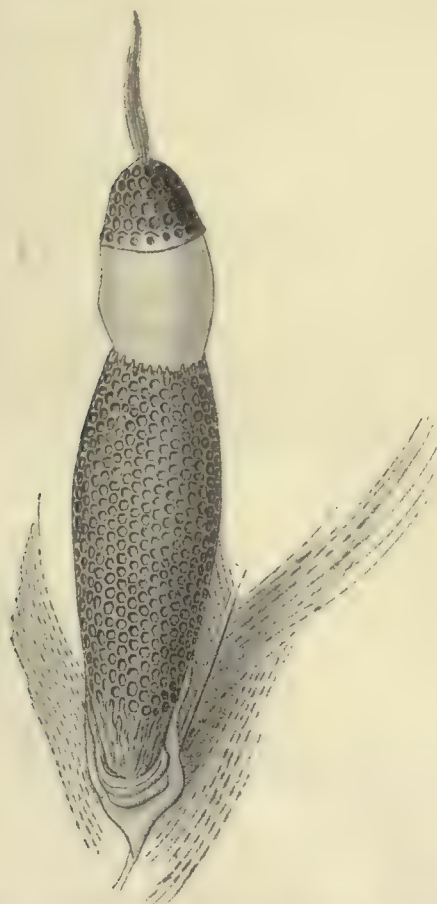


FIG. 4. Egg of *Menopon pallescens*. Nitzsch. Highly magnified. Under the pressure of the cover-slip the operculum has come away and the egg is squeezing its way out of the egg-shell.



FIG. 3. Four eggs of *Goniodes tetraonis* attached to the base of an after-plume. The operculum has fallen off one of them.

GONIODES TETRAONIS.

bristles. The male is readily distinguished from the female by the fact that in it the third joint is produced into an inwardly directed process very like a thumb, and this gives the antennæ a biramous appearance (Pl. LIII., Fig. 1).

The next three pairs of appendages are modified as mouth-parts, and in describing them we propose to mention certain median structures also connected with the mouth.

The most remarkable feature of the under surface of the head of a *Goniodes* is a white cushiony area with the outline of a stout sausage, sometimes described as the "upper lip" or "labrum." It is bounded anteriorly by a ridge of chitin. This cushion is covered with a multitude of rugosities, giving it the appearance of the skin of a dog-fish. There is always a more or less well-marked crease or groove across the long axis of the cushion, and the part posterior to the crease is supported by two longitudinal bars of chitin just as the double banners temperance reformers carry in their processions are supported by the poles.

If one be watching the living *Goniodes* lying on its back on a slide, this cushion will be seen from time to time to swell up and scrape along the under surface of the cover-slip. Then it subsides again, possibly being pulled back by the numerous muscle-fibres which pass back from the anterior end of the head, and which appear to be inserted into the inner surface of the cushion. Along the posterior edge of the cushion is a small mobile membrane or lip which bears a moustache of eight hairs, shorter in the centre, but increasing in length as one passes outward. This lip is frequently drawn down over the tips of the mandibles.

The only function one can suggest for the upper lip is that it acts as a scraping organ, and it may be of use if the animal ever eats the epidermis of its host.

III. *The Mandibles*.—These are by far the most powerful of the mouth-parts, and are very strongly chitinised. The right and left mandibles are not exact images of one another, as the tip of one always closes outside the tip of the other, and thus there is a slight differentiation at the apex, ^{Mandibles.} which is so strongly chitinised as to be almost black. Each mandible is somewhat triangular in shape, the apex forming the tip. The articulation is very complex. A very powerful muscle runs into the external posterior angle of each mandible, the so-called condyle, and serves to bring it into biting contact with the other. The sharp shearing-edge of the mandible is admirably adapted for cutting off the barbules of the feathers which form the food of these biting-lice.

IV. *The First Pair of Maxillæ*.—These are very difficult to see in the living animal and are best observed when in movement. I agree with Grosse¹ in

¹ "Zeitschrift für wissenschaftliche Zoologie," xlii. p. 537, 1885.

describing them as lobes without any traces of palps. They are rounded and bear certain setæ on them. When in motion they are shot up and pulled down between the mandibles and the labium or fused second maxillæ; sometimes both are moved forward at once, sometimes they move alternately.

First maxillæ. *V. The Second Pair of Maxillæ.*—These have fused together and form a labium of a very simple kind. There is a median plate or mentum in which we found no transverse furrow. This plate bears anteriorly a pair of one-jointed processes ending in a few short stiff bristles. These are called by Grosse the paraglossæ, but, as there are a pair of minute one-jointed processes internal to these, it may be that they represent the palps. Whichever they are, they are very mobile, and are constantly being divaricated into a position at right angles to the normal, and then suddenly brought back again. They are obviously of use in bringing food to the mouth. The more median processes as well as the palps bear hairs.

Second maxillæ. A median structure which we think may represent the hypopharynx is the lyriform organ, or the "œsophageal sclerite" of Kellogg. This median piece is strongly chitinised, deep brown in colour, and consequently conspicuous; it seems to lie about in the same level with the first maxillæ, except when they are protruded, when it lies behind them. A muscle on each side of the œsophagus runs from the anterior angle of the sclerite to the dorsal side of the head, and brings about the movement of the organ. Kellogg has described in certain species a pair of oval glands which lie ventral to the sclerite, and the ducts of which unite and open by a common duct into the median groove of the thickening. These glands are very conspicuous in *Goniodes*, and are shown in several of our figures. Their function is unknown. Their ducts are cross-barred like a trachea. The whole sclerite is conspicuous and shines through as a somewhat V- or U-shaped dark area, visible from above. As Kellogg points out, a similar apparatus exists in the Psocidæ. Two salivary glands on each side of the œsophagus have been described in many genera of Mallophaga. The ducts of all four unite and open into the pharynx by a common duct.

The second maxillæ are so minute and feeble that we found it impossible to dissect them out even from macerated specimens.

Prothoracic legs. *VI. The Prothoracic Legs.*—These pair of appendages are turned forward and their ends normally lie underneath the mouth. They doubtless take some part in bringing food to the mouth. Their inner ends are approximated, so that the sternum here is but little more than a line. Snodgrass¹ records that

¹ "Occasional Papers of the California Academy of Sciences," vi. p. 152, 1899.

the prothoracic legs do not move synchronously with either of the others or with each other. One often moves backward as the other moves forward, and he holds that they serve to guide the body. He thinks they serve to pull the body up the feather, the prothoracic legs pulling whilst the other legs push, like a man climbing a rope.

VII. *The Mesothoracic Legs*.—These are larger than the preceding, and are directed backwards; their bases are further apart. The details are shown in Fig. II. All the legs end in claws and bear a well-marked pulvillus. Mesothoracic legs.

VIII. *The Metathoracic Legs*.—These are still larger and, like the preceding, are directed backwards; the sternum between their bases is rather wider. The right and left mesothoracic legs move forward simultaneously and backward simultaneously, and so do the right and left metathoracic legs; but when the mesothoracic legs move forward the metathoracic legs move backwards, and *vice versa*. Metathoracic legs.

In their general structure there is little beyond size in which the legs differ. Each consists of a coxa firmly applied to the ventral surface of the thorax; it is a broad, short piece, wide distally. The second article is a small trochanter which joins the hinder end of the wide coxa and seems to be almost part of the femur, but there is a marked thinning of the cuticle between it and the femur and a clear joint. The femur with the trochanter and the next article or tibia are of about equal length, but the tibia is not so stout; distally it bears a pair of stout bristles, hardly moveable, against which the tarsal claws work. There are other bristles on the tibia, and numerous hairs on all the articles. The tibia bears a single-jointed tarsus which carries a pair of very mobile claws. These claws are constantly being depressed, usually one at a time, and rub against the tibial bristles. The tarsus always carries numerous knobs, and between the base of the claws a pulvillus may be seen; this in some cases is retracted.

The female has no external organs of reproduction, but on the seventh segment of the male there are situated ventrally a couple of complicated gonapophyses which presumably are modified abdominal appendages.

The tracheal system of *Goniodes* opens on the exterior by seven pairs of stigmata. There may possibly have been more, but we could not detect them. The most anterior is the largest; it is situated close behind the first pair of legs, and is very difficult to see. Snodgrass¹ has described one in a similar position in *Menopon titan*. From it a trachea passes inwards and gives off a twig to the second leg. Respiratory system.

¹ "Occasional Papers of the California Academy of Sciences," vi., 1899.

The abdominal stigmata are twelve in number, there being a pair on the second to the seventh segment, both included. They lie on little eminences, like a tee on a teeing-ground, situated about one-sixth of the body-breadth from the edge, and from each is given off a short trachea which soon splits into two branches. Of these the posterior splits up into innumerable fine twigs, which supply the various organs of the segment, and the anterior runs almost straight into the longitudinal trunk, thus placing the system connected with one stigma in communication with all the others on the same sides of the body. By this means, if one stigma be blocked the organs it supplies are not deprived of air, but receive it from another system. The smaller tubes on each side pass across the middle line, and seem to place the right and left systems in communication. In *Menopon titan*, according to Snodgrass, the right and left systems communicate by means of a large transverse trunk in the fourth abdominal segment. The spiral thickenings are well marked.

Grosse has described just within the mouth a dorsal and a ventral piece of a
 Alimentary canal. "Schlundskelet." Unless the lyriform organ, or "oesophageal sclerite," represents the ventral piece, this structure is not evident except in sections.

The oesophagus is a simple tube with muscular walls which traverses the posterior part of the head and the thorax. Soon after it reaches the abdomen it gives off a blind pouch or crop, which is always choked with feathers, and forms the conspicuous black patch which shines through the wall of the abdomen. The walls are very muscular, both longitudinal and circular muscle-fibres being conspicuous. It usually lies near the middle line, but somewhat obliquely, and pointing posteriorly to the right. Behind the point where the crop is given off the stomach or chylic ventricle passes backward, lying to the right of the crop. At the posterior end of this the four Malpighian tubules arise, and then there follows a short intestine in which usually masses of undigested feather-fragments are to be seen. The intestine is short, and ends in a ring of six almost spherical bodies. Each of these seems to consist of a single gigantic cell, and the whole is very richly supplied with tracheæ. These bodies closely resemble similar structures found in the rectum of many Diptera, e.g., the blow-fly and the mosquito. Behind them there is a short rectum, which ends in an anus situated beneath the terminal plate. Numerous muscles run from the body-walls of the last two segments to be inserted into the rectum, and doubtless act as divaricators.

The excretory system consists of (a) the Malpighian tubules, and (b) the fat-body, in which nitrogenous waste matter is often stored away. The
 Excretory system. Malpighian vessels are four in number; they arise at the interior end

of the intestine, and near the base each swells into an oval vesicle. The tubules are long, as long almost as the body, and are coiled away amongst the viscera.

The fat-body is very definitely arranged, there being paired pouches of it at the sides of each segment. In the cavity of these pouches are five collections of oval structures, which may be the five pairs of ovarian tubules, showing the ova, but somewhat similar structures occur, in equal numbers, in the male abdomen.

We have not made a detailed examination of the nervous system, but may remark that it consists of a brain and a large infra-oesophageal ganglion in the head and of three ganglia in the thoracic segments. The last of these is the largest, and it supplies nerves to the organs of the abdomen.

This, again, we have not examined, but Wedl¹ and Kramer² have seen and described, the hearts of several species. They seem to conform to the usual insect type, but the number of chambers is small, Wedl says only one in *Menopon pallidum*, situated in the last abdominal segment but one.

We have not investigated the reproductive organs in any detail, but it may be mentioned that in the Ischnocera, the subdivision of the Mallophaga to which *Goniodes* and *Nirmus* belong, there are four testes, the two on each side being united by a common vas deferens, which leads into a vesicula seminalis, which, though bilobed, is usually unpaired; from this an ejaculatory duct leads to a retractile penis. Morphologically there is an invagination of the body-wall of the last abdominal segment to form the genital cavity, and the various plates and bars are chitinous thickenings in the walls of the invagination. In the centre of the genital cavity lies the penis, which is strengthened by chitinous rods and bars, and is capable of being protruded and retracted by a complicated system of muscles. In the male the anus has been involved in the invagination and comes to open dorsally into the genital cavity. This is not the case in the female, where the invagination is not close to the posterior end, but is formed by an invagination of the eighth abdominal segment. The vagina opens anteriorly and dorsally into this chamber, and passes into a long coiled oviduct which splits into two collecting-ducts, and these terminate in five ovaries on each side of the body. The ovaries dwindle out anteriorly, and their thread-like forward ends unite into a common termination.

An excellent comparative account of the reproductive organs of the group is

¹ "Sitzungsberichte der mathematisch-physikalischen Classe der Kaiserlichen Academie de Wissenschaften xvii. Vienna.

² "Zeitschrift für wissenschaftliche Zoologie," xix. p. 452, 1869.

given in Snodgrass's already mentioned paper, and Gross¹ has written an account of the histology of the ovary, which he finds strikingly like that of the Pediculidæ.

The eggs are very beautiful objects; in badly-infested Grouse they may be numerous, but as a rule they were none too easy to find. Usually they occur in small groups attached to the base of the after-plume and between it and the shaft of the plume. The specimen figured was on one of the feathers from the flank (Pl. LIII., Fig. 3).

The eggs are elongated, some three to four times as long as they are broad. They are fixed by some adhesive secretion at the end corresponding to the posterior end of the contained embryo. At the other end is a well-marked cap or operculum, which always points to the free end of the feather. The beauty of the reticulated egg-case is shown best in the genus *Menopon*, and we figure one, which we take to be the egg of *Menopon pallescens* Nitzsch, found on the feathers of a partridge (Pl. LIII., Fig. 4). Under the pressure of a cover-slip the egg-case gradually ruptured along a circular line below the well-marked thickened edge or rim of the operculum. The contained egg then began to emerge, carrying the operculum as a sort of cap, the resemblance to which was emphasised by the long process which stands out like a feather borne on the apex. The eggs of *Goniodes* show the reticulations less well, but they are well marked on the operculum, which bears a long tapering filament, longer than the egg itself. They also occur just below the opercular rim, but fade away towards the fixed end. The general appearance of the eggs in the after-plume is shown in Pl. LIII., Fig. 3. They were found on July 27th, 1908, and they seem to be laid throughout the summer.

There is no metamorphosis, the young leaving the egg-shell as a miniature of their parents.

II.—*NIRMUS CAMERATUS* Nitzsch.

This insect seems to have been first named by Nitzsch² in the year 1818, but with no description. Indeed, the animal is mentioned under the subgenus *Nirmus*, but is called *Philoptyerus cameratus*. It is figured and described, and a bibliography is given, in Denny's "Monographia Anoplurorum Britannicæ,"³ under the name of *Nirmus cameratus*. Denny found it on the Red Grouse, the Black Grouse, "and I expect also on the Ptarmigan." Grube describes it in Middendorff's "Siberian

¹ "Zoologische Jahrbücher, Anatomie," xxii. p. 347, 1905.

² Germar's "Magazin der Entomologie," iii. p. 291. Halle, 1818.

³ London, 1842, p. 112.

PLATE LIV.

NIRMUS CAMERATUS.

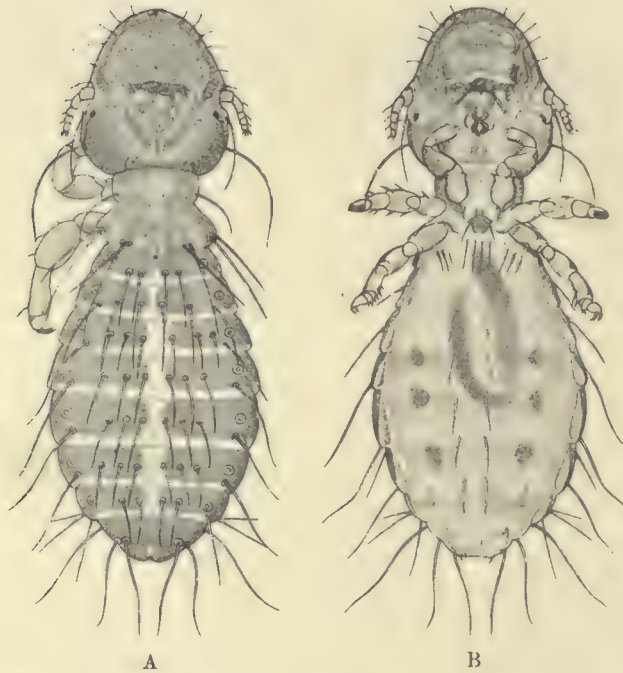


FIG. 1. *Nirmus cameratus*. Nitzsch. Magnified. Female. A seen from above; B seen from beneath.



FIG. 2. Eggs of *Nirmus cameratus* on the feathers of a young Grouse about three weeks old. A, very slightly magnified, three eggs on one of the wing-covers; B, magnified about eight times, one egg on a downy plume; C, very highly magnified to show reticulations.

Travels" as existing on *Lagopus albus* and *L. alpinus*, thus confirming Denny's surmise.

It is mentioned in Giebel's article¹ on the Halle Bird-lice, and described and figured in his great monograph "Insecta Epizoa."—Piaget, in his "Les Pédiculines," states his conviction that *N. cameratus* is specifically identical with the *N. quadrulatus* of Nitzsch, from *Tetrao urogallus*, the Capercaillie. Kellogg in his Mallophaga ("Genera Insectorum") does not mention *N. cameratus*, though he records *N. quadrulatus* from *T. urogallus*, *T. tetrix*, and *Lophophorus impeyanus*.

Nirmus is a more slender animal than *Goniodes*, and appears to be longer. It is rarer than the latter, though in the great majority of cases the two are found together. Most of what has been said above about *Goniodes* applies also to *Nirmus*, as their habits are very similar, except that *Nirmus* lives more on the skin and upon the base of the rachis of the feather than does *Goniodes*. It also seems to frequent the feathers under the wing, where *Goniodes* is seldom seen. Both species seem to wander all over the body; and though they seem rather more common upon the head, neck, and back, the old view that these biting-lice occur chiefly or exclusively on those parts of the body inaccessible to the beak was not borne out by our investigations.

The variation in size and in colour is very considerable. Dead specimens are not infrequently found, and these may be in some cases mistaken for cast skins. An average length is 3 mm., and an average width of the abdomen is 1.5 mm. The abdomen is the widest part (Pl. LIV. Fig. 1). In no case did we find either *Goniodes* or *Nirmus* in the crop of the Grouse, though, as we have just stated, they are fully exposed to being snapped up by the bird's beak if the bird cared to notice them. It is not known exactly how clean birds get infected: probably the Mallophaga simply crawl from one bird to another when the latter are contiguous, and the young birds are infected on the nest. There is evidence, however, that in some cases, probably rare ones, they cling to the Grouse-fly, and are by it transported to a new host.

In the summer of 1907 Mr Fryer found some Mallophaga eggs. These were for the most part empty, but from one or two full ones he has succeeded in hatching out specimens of *Nirmus cameratus*. The eggs are white, and trans-^{Eggs.}parent when empty, just visible to the naked eye, 0.6 mm. in length, and about four times as long as they are broad. Each egg-case is beautifully reticulated, the areas between the reticulations being six-sided. At one end the egg has

¹ "Zeitschrift für gesammten Naturwissenschaft," xxviii. p. 370, 1866.

a cap which is pushed off when the young emerges. The eggs are laid between the barbules of the vanes or near the bases of the filo plumes, and adhere to their supports by means of some sticky excretion (Pl. LIV., Fig. 2).

The eggs appear to be laid throughout the summer; the first time we found them (some of them were empty) was on July 2nd, 1907, and we found others later in the season.

There is no metamorphosis; the young emerge from the egg-case as small miniatures of their parents. They seem to cast their skin several times; but the exact number of ecdyses is not known.

B. DIPTERA.—Flies.

(i.) Fam. Hippoboscidae.

III.—*ORNITHOMYIA LAGOPODIS* Sharp.

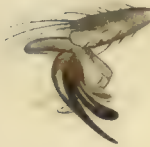
Till recently it had been thought that the Grouse-fly was the same species as the common bird-fly, *Ornithomyia avicularia* L.; but recently Mr D. Sharp¹ has pointed out that it is a distinct species, which he has described, as follows, under the name of *O. lagopodis* (Pl. LV.):—It is “smaller than *O. avicularia*, and distinguished by its peculiar lurid blackish colour, without any trace of green even on its feet or legs; the rostrum is black, and the hairs of the body and appendages are shorter than in the better-known form; on each side of the thoracic pleuron, between the front and middle legs, there is a very large dark patch extending as far towards the middle as the base of the front coxa, and divided into two parts by an oblique pallid line. The head is considerably smaller and narrower than that of *O. avicularia*, and has beneath a very large area of smoky colour on each side. Mr Colin has pointed out that the segments, or abscissæ, of the costa afford a good character; the relative lengths of the outer two being in *O. lagopodis* as 9-8, and in *O. avicularia* about 12 or $12\frac{1}{2}$ -8. The bristles on the scutellum are usually more numerous, as well as larger, in *O. avicularia*.” Recently a second species *O. fringillina* Bezzi, has been separated off from the *O. avicularia*, so that we now have three species of *Ornithomyia* in this country, and probably more will be added as the group is further studied. Mr Sharp thinks that the same species frequents the Willow-Grouse, *L. albus*, of Scandinavia.

The head and mouth-parts of this fly are very interesting. A ventral view shows, between the eyes, the short antennæ apparently of two joints, ending in

¹ *Entomologists' Monthly Magazine*, II., ser. xviii. p. 58, 1907.



A.



C.



B.

21.

ORNITHOMYIA LAGOPODIS.

E. Wilson, Cambridge

four hairs, of which one is far longer than the others; other symmetrically arranged hairs also occur. In the middle line is the proboscis; this consists of two lateral, moveable, palp-like structures, each bearing hairs and terminating in a stout bristle. These structures are presumably the maxillary palps. Then there is a median very mobile structure, which is the sucking tube; this moves in all planes, and may be protruded or withdrawn. Its mouth shows a somewhat plicated orifice, and behind it undoubtedly ends in a sucking pharynx. This median structure is probably homologous with the second maxillæ or the labium.

The feet of the Grouse-fly are large but very beautiful. In Pl. LV., Fig. c., will be found a coloured sketch of a foot seen obliquely. From this drawing it will be seen that the large paired claws are double, and that whereas the distal limb of each claw is slender, and very sharply pointed, the proximal limb is much stouter and ends bluntly. Between the claws is a median, feathered process with hairs or bristles, and at the base of each double claw is a pulvillus covered with minute hairs.

We do not know the exact relations of the Grouse-fly to the Grouse. It is believed to suck its blood, and it will certainly bite human beings. For a time it seems to burrow amongst the feathers of the bird, and any one handling Grouse during the summer is likely to disturb a fly or two. They come buzzing out, and are apt to crawl up one's sleeve by aid of the pair of great hooked claws on their feet. Altogether they have a sinister aspect, and to people who do not like flies they are very repellent. They occur freely in larders where freshly-killed Grouse have been placed, and after a short time they leave their dead host and accumulate upon the windows.

The earliest month in which we have found the Grouse-fly is June. The latest we have found it up till the present time is September. In Caithness they have been taken as late as October. Perhaps they are most plentiful in August.

The females seem to be commoner than the males, or, it may be in August they are more readily taken. Like other members of the Hippoboscidae, which includes the horse-fly, forest-fly, and sheep-tick, the Grouse-fly does not lay eggs, but the ovaries produce one large ovum at a time, and this passes into a dilated oviduct which acts as a uterus, and here the egg develops. After attaining a certain stage of development, the larva surrounds itself with a pupa-skin, and is extruded. The chitin covering the larva hardens and blackens with exposure to the air, and forms the so-called pupa-case; in fact, one may almost say the young are hatched as pupæ. At no time is the larva exposed, though there is a larval stage free in the uterus wrapped first in the egg-shell and then in the pupa-case.

When first deposited the pupæ are light in colour, and the case has not hardened. Those dissected out from a fly are shorter and more squat than the mature pupæ found on the ground, and the symmetrical ridges and elevations are much less well marked.

The pupæ were found during August and September. They appear to be deposited amongst the feathers, and are easily detached from them. The few we have found either dropped on some paper over which we were handling some birds, or lay loose at the bottom of the cardboard boxes in which Grouse travel. Probably they take some eight or nine months before they give rise to the imagos, and the latter very likely disappear altogether from about October till June. Further research is needed to throw light on these questions.

Three specimens of *O. lagopodis*, all of them taken from one Grouse, were themselves markedly infested with an ectoparasite, a species of mite. Here I refrain from quoting Dean Swift. The mite belongs to the genus *Canestrinia*, as my friend Mr C. Warburton has kindly told me, and is probably a new species. The subfamily Canestrininæ are all parasitic upon insects, and are regarded as harmless. Our specimens existed in considerable numbers, clustered round the hinder end of the fly's abdomen on the ventral surface, with their proboscides plunged into its body. Many were laying eggs, and many cast-off cuticles were lying around. Eggs from which the larvæ had escaped presented a spindle-shaped outline; others contained ova in various stages of differentiation; others fully formed larvæ.

We have in no single case found a Grouse-fly in the crop of a Grouse, nor have we yet found any cestode larvæ or cysts in the bodies of the flies which we have cut into sections or dissected.

(ii.) Fam. Scatophagidæ = Scatomyzidæ.

IV.—*SCATOPHAGA STERCORARIA* L.

This fly cannot be looked upon as an ectoparasite of the Grouse, but it lays its eggs in Grouse-droppings, and its maggots live on and in these dejecta. The maggots must therefore constantly be in close contact with and possibly eating the ova of the tapeworms which exist in such vast numbers in the Grouse-droppings; and hence we thought it was a profitable object to investigate for the cysticercus or second stage of the cestode. It should be mentioned that the droppings consist of two parts: (1) the dejecta from the intestine strictly speaking, and (2) the more

CERATOPHYLLUS GALLINULÆ, ETC.



Fig. 1. The Grouse-fly *Ornithomyia lagopodis*.
Magnified about nine times.



FIG. 2. Larva of *Scatophaga stercoraria* L. From a Grouse-dropping. Magnified.
a.s. anterior spiracle.
p.s. posterior spiracle.
h.s. hypostomal sclerite.
ph.s. pharyngeal sclerite.
v.t. visceral trachea.
t.c. transverse commissure.



A



B

FIG. 3. Side view of *Ceratophyllus gallinulae*. Dale. Highly magnified.
A, Male; B, Female drawn to the same scale and showing the relative difference and size.

fluid dejecta from the cæca. The latter pass last, and often lie like a cap upon the former. The fly-maggots are only found in numbers in the "cæcal" part of the dropping. Mr Fryer first found them commonly at Fort Augustus in April. In June they were not so common, owing perhaps to the rain, which washed the cæcal part of the droppings away. We examined a large number of the larvæ both by squashing them and cutting them into sections, but we found no trace of infection; in fact, here, in this most likely place, we again drew a blank. No specimen of *S. stercoraria* or of its larvæ has been found in the crop. This fly, which, as stated above, we believe to be *S. stercoraria*, may eventually turn out to be a local variety.

The larva of the fly has the usual maggot-like shape, tapering from behind forward towards the mouth. Counting what appears to be the cephalic segment—but which in reality probably represents more than one segment, and which is thus conveniently called the "pseudo-cephalon"¹—as one segment, there are thirteen in all, the usual number for Dipterous larvæ (Plate LVI., Fig. 2).

The cuticle is thin, the maggots are white. They bear numerous small spines, which are especially conspicuous in a ring around the anterior end of each segment. These rings emphasise the segmentation of the larva.

The "pseudo-cephalon" is pointed, and varies in outline according to the extent of protrusion of the mouth and its sclerites. These sclerites are the most conspicuous structures in the larvæ; jet-black, they stand out against the white tissues of the maggot. There is a pair of hooks which apparently correspond with the single median mandibular sclerite of *Musca domestica*.² At the base of each of these is a dentate sclerite, and the mandibular sclerite articulates behind with the hypostomal sclerites. These latter are irregular longitudinal bars connected by a slight transverse plate on the ventral side. In *M. domestica* the salivary glands open into the pharynx just in front of the transverse piece. Posteriorly the hypostomal sclerites are very closely articulated, or perhaps even fused with the large lateral pharyngeal sclerite. This consists of a ventral plate, continuous with two lateral plates which are deeply notched, and in the house-fly the nerves and tracheæ which supply the pharynx enter through this notch. The two lateral plates are united anteriorly by a dorsal cross-piece. The whole of these sclerites are being continually pushed forward and retracted by a complicated series of muscles which have been carefully described in the case of *M. domestica* by Dr C. Gordon Hewitt.

¹ L. F. Hennequy, "Les Insectes," Paris, 1904.

² C. Gordon Hewitt, *Quarterly Journal of Microscopical Science*, lii. p. 495, 1908.

The mouth is bordered by tumid lips, above which the hook-like mandibular sclerites are pulled and pushed in and out. Dorsal to these again are two elevations which each bear two sensory papillæ; these correspond with the sensory tubercles of *M. domestica*, though the latter are not borne on an elevation.

The anus opens on the truncated thirteenth segment, well forward on the ventral surface; around it, symmetrically placed, are four anal papillæ, which assist in the movements of the maggot.

The tracheal system opens on the flattened posterior end, about the centre. Ventral to the stigmata there are two or three pairs of low papillæ. Each stigma leads into a trachea, which almost immediately divides into a visceral branch which bends down into the viscera and extends a little way in front of the middle of the body. Before splitting in *M. domestica* the right and left main trunks are put into communication by a transverse trunk; if this exists in *S. stercoraria* it escaped our notice. The lateral trunks give off in each segment a dorsal and ventral twig. Anteriorly, in what appears to be the third segment (it is described as the fourth in the house-fly), there is a transverse commissure by means of which the right and left trunks are put into communication. In front two small twigs are given off from this transverse commissure which run to the pharynx. The main trunk is continued forward, and at the second segment (the third in the house-fly) it ends in a process like a little rake. This is due to the splitting up of the trachea into eight or nine little twigs, all in the same plane and all ending in a knob. The whole is called the anterior spiracle, and can be protruded from the body and retracted. Hewitt states that in the house-fly each of these knobs opens to the surface by a very minute pore.

C. SIPHONAPTERA.—Fleas.

(i.) Fam. Pulicidæ.

V.—*CERATOPHYLLUS JALLINULÆ* Dale.¹

Synonym : *Ceratophyllus (Trichopsylla) newsteadi*² Rothschild.

I am indebted to my friend Mr N. C. Rothschild for identifying this flea, which is here recorded for the first time from the Grouse. It is a well-known bird-flea, having been found in the nest of the hawfinch, *Coccothraustes vulgaris*, in that of the dipper, *Cinclus aquaticus*, in that of the blackbird, *Turdus merula*,

¹ N. C. Rothschild, *Entomologists' Monthly Magazine*, II., ser. xiv. p. 145, 1903.

² *Entomologists' Record*, xiii. p. 284, 1901.

the moor-hen, *Gallinula chloropus* L., and others. In the thousands of Grouse which have passed through our hands we have found but one or two specimens of this flea, all in 1906, and we have never found a single specimen in the crop. The dog-flea, *Pulex serraticeps* P. Gerv., is said to be the intermediate host of the dog tapeworm, *Dipylidium caninum*, and, as Dr Leiper suggests, it may be that the *C. gallinulæ* plays a part in the life-history of the Grouse tapeworms. In identifying a flea almost every hair tells, and, as *C. gallinulæ* has not been accurately figured before, I take this opportunity of figuring it in both sexes (Pl. LVI., Fig. 3, A and B).

VI.—*CERATOPHYLLUS GAREI* Rothsch.

This second species of flea was found in a Grouse in 1907; we only took one or two specimens. It is recorded by Evans¹ from the nest of the water-vole, of the lapwing, *Vanellus vanellus*, and of the ring-dove, *Columba palumbus*. Rothschild² has found it in the nest of a water-hen, *Gallinula chloropus*, and he records it as having been taken from *Mustela erminea*, the stoat, *M. vulgaris*, the weasel, *Sorex vulgaris*, the shrew, *Microtus glareolus*, the bank-vole, and *M. amphibius*, the water-rat, and from hedge-clippings.

ARACHNIDA.

ACARINA.—Mites and Ticks.

(i.) Fam. Ixodidæ.—Ticks.

VII.—*IXODES RICINUS* (L.)

This is one of the commonest and one of the oldest known ticks of Europe. In the British Isles it usually occurs on hunting-dogs, and is sometimes called the "dog-tick"; the adult stage is especially frequent on sheep, goats, and oxen, less common on horses, dogs, and men. Mr William Evans³ tells me that he has not found this species on dogs—in his district the "dog-tick" being *Ixodes hexagonus* Leach, var. *inchoatus* Neum. On the other hand, the larvæ and the nymphs are common enough on birds, lizards, and small mammals—in fact, on animals which live among and brush against grass or heather. It is only in the nymph and larva state that we found these ticks on the Grouse. On each of the infested birds the

¹ "The Annals of Scottish Natural History," p. 163, 1906.

² *Entomologists' Monthly Magazine*, II., ser. xiii. p. 225, 1902.

³ "The Annals of Scottish Natural History," p. 35, 1907.

specimens were fixed on the chin or around the eyelids—in fact, in such positions as the Grouse cannot reach with its beak. In parts of Ross-shire, especially in certain woods, these ticks swarm in enormous numbers, and the keepers assure us that they kill large numbers of young blackgame. Hence there is nothing remarkable in finding this species from time to time on the Grouse, where its presence must be regarded as accidental. The larval stages emerge from the eggs, and probably crawl on to the heather, and thence on to the Grouse or other animals which come in contact with the vegetation. We have found both larvæ and nymphs amongst the feathers, but in small quantities and on rare occasions. We have never found it in the crop, and it can hardly play any part in infecting the bird with tapeworms.

Ixodes ricinus, or the “castor-bean tick,” as it is called in America, is common in many parts of the world. It is reported from sheep, goats, cattle, horses, deer, dogs, cats, foxes, ferrets, hedgehogs, hares, rabbits, bats, birds, and man. This tick occurs most frequently during the spring and early summer, but can be found in lesser numbers up till September and October, possibly later.

Severe epizootics amongst fowl of spirillosis and of another obscure but very often fatal disease have been described by Balfour¹ in the Sudan. The spirochæte, probably *Spirochæta gallinarum*, which causes the first-named disease is transferred from one fowl to another by a tick, *Argas persicus*. The second, and as yet rather obscure, disease is recognised by the natives, and by them associated with the presence of the *Argas*. We have found no traces of such disease in Grouse, and the recorded number of ticks taken in the Grouse is, except locally, so small that they can hardly play any part in “Grouse Disease.”

(ii.) Fam. Tyroglyphidæ.

VIII.—*ALEUROBIUS FARINÆ* (De Geer).

Synonym: *Tyroglyphus farinæ* Gerv.

Mr C. Warburton has kindly identified for us a small mite which was found in considerable numbers on several birds and at varying times of the year. Whilst very common at Easter time, they were less abundant in July. *Aleurobius farinæ*, sometimes known as the flour-mite, occurs in great numbers on all sorts of organic material—grain, straw, hay, tobacco, flour, cheese, dead bodies, etc., etc. At times workmen handling corn, cats, horses, etc., have suffered much cutaneous irritation

¹ *British Medical Journal*, No. 2445, p. 1330, November 9th, 1907.

and eruption from the attacks of this mite. There seems no doubt as to the species of this mite, but the authorities on these animals express surprise that they should occur so commonly on the Grouse. Our specimens, some of which were taken on freshly killed Grouse, contained some red substance in the stomach, probably blood from the bird. There seems at present little reason to incriminate this mite as the carrier of the tapeworm cyst. They were, however, found by Mr Fryer on a large majority of birds which were especially searched with the view of finding mites.

(iii.) Fam. *Gamasidæ*.

IX.—*GAMASUS COLEOPTRATORUM* (L.).

We have also taken this common, fawn-coloured mite off the feathers of a Grouse. It is usually found on beetles, but winters under stones, and it is said to die soon if removed from the beetle or from under the stone where it hides, unless it is kept moist. The beetles it favours are usually burrowers in the damp ground or under cow-dung. It probably passes on to the Grouse from under stones.

GENERAL DISCUSSION ON THE RELATIONS OF ECTOPARASITES
TO THE ENDOPARASITES OF THE GROUSE.

We have in the alimentary canal three species of tapeworm, two of the genus *Davainea* and one of the genus *Hymenolepis*. We know that tapeworms, with perhaps the exception of one species, pass through two distinct and different animals known as hosts. In one animal the parasite lives as an adult, in the other as a larva. The larval host is always, sooner or later, eaten by the host of the adult, and then the larval tapeworm or cyst grows into the adult tapeworm. It was with the hope of discovering the second or larval host of the Grouse cestodes that we began a laborious research on the insects and arachnids which infest the Grouse. Unfortunately, little or nothing is known about the life-history of any species of either *Davainea* or *Hymenolepis*. The larval or cystic stages of the former have in some few cases been said to occur in insects and in molluscs; the larva of the latter is thought to live in an insect or a myriapod, or perhaps even more likely some "water-flea" or other fresh-water crustacean.

With regard to these possible second hosts; we have never found a myriapod in the crop of a Grouse, and so far we have not found any crustacea—though it

must not be forgotten that these are probably so small as to escape notice. We have found in the crop of a Staffordshire Grouse one species of slug which Mr W. E. Collinge has kindly identified for us as *Arion empiricorum* Férussac, a species of slug which is common on the Staffordshire Grouse-moors. He tells me that the slug undoubtedly belongs to the genus *Arion*, and almost certainly to Férussac's species *A. empiricorum*, a name included by J. W. Taylor in his "Monograph of Land and Fresh-water Mollusca of the British Isles,"¹ among the synonyms of *Arion ater* (L.). The well-known difficulty of identifying slugs which have been preserved and which have lost their colour accounts for the slight doubt that exists. *Arion empiricorum* is very voracious and practically omnivorous; it will eat almost anything, especially decaying animal and vegetable matter, fungi, paper, weak and injured worms and slugs, and—what is interesting from the point of view of the Grouse tapeworms and roundworms—it devours the dejecta of other animals. It prefers the shady places in moors and fields, and emerges into the open only at dusk or when the day is cloudy or overcast. The following parasites which may give rise to adult forms in the Grouse have been found in *A. empiricorum* :—

TREMATODA (Flukes) :

- (1) *Cercariacum limacis* Duj.²
- (2) *Cercaria trigonocerca* Dies.

CESTODA (Tapeworms) :

- (1) *Cysticercus arionis* v. Sieb.
- (2) *Cysticercus taniæ arionis* v. Sieb.

NEMATODA (Roundworms) :

- (1) *Leptodera angiostroma* Duj.
- (2) *Leptodera appendiculata* Schneider.
- (3) *Nematodum limacis atra* v. Sieb.
- (4) *Pelodytes hermaphroditus*, Schneider.

We have cut one of these slugs into sections, and have sought diligently through them for cysts of tapeworms, but have found none. This absence of infection, combined with the great rarity of the slug in the Grouse's crop, seems to show that *A. empiricorum* is not the second or larval host of the Grouse cestodes.

¹ Leeds, Part XI. p. 167.

² Full references to the literature where these are described are given in my original Paper in the *Proceedings of the Zoological Society, London*.

Dr Wilson and Mr Fryer "tow-netted" some of the moor streams in April 1907, and found a certain number of the nauplius larva, probably of *Cyclops*, and a certain but small number of adult *Cyclops*. The numbers were, however, meagre, and tow-nettings later in the summer yielded an even more unsatisfactory "bag." None of the crustacea when examined microscopically showed any cysts, and as they were few in number and quite cystless, it seems improbable that the source of the tapeworm infection lies here.

Mr D. J. Scourfield, who kindly looked through some of these tow-nettings, tells me he found the following species of Entomostraca:—

CLADOCERA.

Chydorus sphaericus (O. F. M.), the most abundant form.

Alonella nana (Baird, Norman & Brady), frequent.

Alonella excisa (Fisch.), frequent.

Acantholeberis curvirostris (O. F. M.), a fair number, with some cast ephippia.

COPEPODA.

Cyclops nanus Sars, a few.

Cyclops languidus Sars, a single specimen only seen.

Cyclops vernalis Fisch., again only one specimen was seen.

I subjoin three more lists of tow-netted fresh water Entomostraca from three different lochs. These were collected and identified by Mr Wm. Evans, who has kindly put them at my disposal, and they clearly indicate the sort of surface fauna which may be obtained from the lochs on the Scotch moors in early autumn.

LIST I.

From Loch Rusky, a moorland loch a few miles from Callander, which was tow-netted on September 16th, 1906.

CLADOCERA.

Simosa vitula (O. F. M.).

Eurycercus lamellatus (O. F. M.).

Alonopsis elongata (G. O.) Sars.

Alona affinis Leydig.

Chydorus sphaericus (O. F. M.)

OSTRACODA.

Cyclocypris globosa (G. O. Sars).*Pionocypris vidua* (O. F. M.).*Notodromus monacha* (O. F. M.).*Candona candida* (O. F. M.).

COPEPODA.

Moraria brevipes (G. O. Sars).*Cyclops viridis* (Jurine).*Cyclops annulicornis* Koch.*Cyclops serrulatus* Fischer.

LIST II.

From Peat-pools on Grouse moors on Ben Ledi, in South-West Perthshire,
September 1908.

CLADOCERA.

Chydorus sphaericus (O. F. M.), very abundant.

OSTRACODA.

Herpetocypris tumefacta (B. & R.).*Cypridopsis villosa* (Jur.).*Potamocypris fulva* (Brady).*Candona candida* (O. F. M.).

COPEPODA.

Attheyella zschokkei (Schm.).*Attheyella cuspidata* (Schm.).*Cyclops vernalis* Fisch.

LIST III.

From Loch-a-Chroin, north of Callander.

CLADOCERA.

Bosmina longirostris (O. F. M.).*Acroperus harpæ* Baird.*Alonopsis elongata* (G. O. Sars).*Alona quadrangularis* (O. F. M.).*Alonella excisa* (Fisch.).*Chydorus sphaericus* (O. F. M.).

OSTRACODA.

Cyclocypris serena (Koch).

COPEPODA.

Diaptomus gracilis (G. O. Sars).

Cyclops viridis (Jur.).

Cyclops serrulatus Fisch.

Also the common fresh-water Amphipod, *Gammarus pulex* (De Geer.)

A complete list, so far as was known at that time, of the Entomostraca of the Highlands and of the Lowlands could be extracted from the very useful Synopses published by Scourfield in the *Journal of the Quekett Microscopical Club* during the years 1903 and 1904.

In none of the species examined have we yet succeeded in finding any cysts.

We have thus with some degree of probability shut out as the second or larval host of the tapeworms—at any rate for the present—the ectoparasites of the Grouse, the myriapoda and the slugs or snails, and the fresh-water crustacea, and this on the grounds (1) that on examination none of them reveals a cyst, and (2) that these animals are either not eaten by the bird, or so rarely eaten and in quantities so small as to render it highly improbable that any of these invertebrates could account for the almost constant presence of the cestodes in large numbers in the Grouse.

Two rather striking facts seem to point to the normal insect food of the Grouse, which it picks up on the moor, as the more probable source of the tapeworms. One is that two of the artificially reared Grouse at Frimley, which died during the early autumn of 1907, were carefully searched for tapeworms, but neither *Davainea* nor *Hymenolepis* was found. The second fact is that young Grouse often contain fully-grown *Davainea* before they are three weeks old. They must certainly have swallowed the second host when very young, perhaps even the day they were hatched, or the worm would not have had time to grow. Hence our best chance of finding this second host is to examine the crop-contents of the very young birds, and to do this we must have a moor at our disposal, and leave to kill as many young birds as we may want.

I have been assured over and over again by sportsmen and gamekeepers that the Grouse eats no insects; but this is far from the truth.

Although the observations on the animal food of Grouse are still incomplete, enough has been done to show that it is fairly abundant and very varied. A fuller report on the insects found in the Grouse-crop is given by Mr J. C. F. Fryer in the Interim Report of the "Grouse Disease" Inquiry, published in August 1908, and in chapter iv.¹ The following two paragraphs relate to some observations of my own, made in 1905 and 1906.

"From the crop of a single bird I have taken six larvæ of Tenthredinidæ (saw-flies), eight caterpillars of a Geometrid moth, one caterpillar of a smaller moth, two small Tineid moths, a number of immature Homopterous insects resembling the 'frog' or 'cuckoo-spit,' a fly, possibly a *Leptis*, two specimens of the family Aphidæ (plant-lice), one small spider and the remains of four specimens of the slug *Arion empiricorum* Fér. The gizzard of the same Grouse contained, in a more broken-up condition, and consequently more difficult to identify, two or three dozen larvæ of saw-flies and moths, some young Homopterous insects, and the pupæ of two Muscid flies.

"The segments of the Grouse tapeworms containing the ripe eggs pass away with its dejecta and get on the ground or on to the heather and other plants, or into water. The eggs of the two species of *Davainea* are believed to develop into the cestode larva inside the body of an insect or a land mollusc. They are excessively minute, and lying as they do, in millions on the heather, may be readily consumed by the leaf-eating caterpillars and other insect larvæ which live on the moors. Doubtless many are eaten by the Grouse themselves, but they are digested and come to nothing. As we have said above, a tapeworm must have a second or intermediate host, and its larval stage must be passed inside an animal quite distinct from that which harbours the adult worm. To get at and eat the eggs seems to me an easier matter for caterpillars and other insect larvæ or for slugs than it is for the ectoparasites, which as a rule are not very likely to come across the dejecta of their host. For this reason, in looking for the larval tapeworm, we have sought the insect larvæ and the slugs eaten so eagerly by the Grouse. A common food of Grouse is the head of certain species of rush. *Juncus articulatus* v. *lamprocarpus*, *J. squarrosus* and *J. effusus* v. *conglomeratus* are all frequently eaten. There is a very minute moth the larvæ of which live in curious, white, papery cases inserted into each twig of the rush-head which they eat. When the rush is in its turn eaten by the Grouse the larvæ of the moth pass into the alimentary canal of the bird and are there digested. It has not been possible to

¹ Chap. iv. p. 88 *et seq.*, vol. ii. Appendix E.

finally determine the species of the moth, but I think it is *Coleophora cæspititiella*,¹ for this species frequents many species of rush ; whereas the *C. glaucicolella*, the other inland species, is most partial to *Juncus glaucus*. The former is usually fully out by the middle of June and lingers on till the middle of July ; the last-named moth issues about the middle of July and flies for four weeks. The case is whitish, semi-transparent, and with brown specks ; it is found when the larva is no longer young, but not at any very fixed time. At first its outer end is closed. The larva often leaves the case, burrowing into the rush-head for food, and at times fails to refind it. Before pupating, the outer or anal end of the case is opened and the case strengthened by a glandular excretion. These larvæ should be searched for cysts.

¹ J. H. Wood, *Entomologists' Monthly Magazine* II., Ser. iii. (xxviii.), 1892.

CHAPTER XVII

MOOR MANAGEMENT

By Lord Lovat

BEFORE going into the question of moor management and the various suggestions that have been brought forward from time to time with the object of maintaining the health of Grouse, it seems advisable to give a brief *resumé* of some of the more important hygienic and economic facts established in the preceding chapters.

Objects
of this
chapter.

New data, intelligently apprehended, must of necessity entail a regrouping of ideas, and it is therefore expedient, in the light of a heightened standard of knowledge, to re-examine old assumptions, sift the good methods from the bad, and look into the why and the wherefore of recognised specifics, before embarking on suggestions as to the lines on which further developments should best proceed.

It is not only in the advancement of abstract knowledge and the co-ordination of existing practice with scientifically established fact that progress is to be made. The results on the practical side should be no less important. In the first place, the keeper is by profession a trained observer, and, as far as the consideration of natural phenomena is concerned, an educated man. Nothing is more likely to act as a stimulus to personal exertion, and therefore to increased attention to the moor, than a clear understanding on his part, not only as to what should be done—of which he has already a pretty thorough grasp—but also as to the reason why a given action is taken about which he has but too often the most vague ideas. Again, if any advance is to be made in methods of moor management, it is obvious that the details must be worked out by the practical man on the spot; this can only be done if the keeper realises the nature of the difficulties to be met, and the reasons for which the suggested remedies are put forward.

In recapitulating certain findings of the Committee it will not be necessary to

go into questions of purely scientific interest, still less to set out again at any length the facts established in former chapters. As far as possible, scientific nomenclature will be avoided, and only such matters dealt with as bear directly on the health of moors.

Briefly stated, the "Grouse Disease" Committee claim to have defined the main—in their opinion the only—primary causes of what is commonly known as "Grouse Disease."

Cause of
"Grouse
Disease."

During the six years of their investigation they have examined outbreaks of disease in every Grouse-producing county of England, Scotland, and Wales.

Work of
Committee.

They have dissected birds, not only in the laboratory, but freshly killed in the vicinity of the moor; they have had the advantage of all the conveniences of modern and recently devised scientific appliances; they have been kept accurately informed of the outbreaks of disease, and by means of a network of correspondents extending to every part of the Grouse area, have been able to observe the epidemic in every phase of its progress.

Apart from these advantages, not enjoyed by any former body of inquirers, the Committee have been assisted by field observers of experience, who have reported and classified variations in local conditions. In the main divisions of research—entomological, pathological, helminthological, parasitical, botanical—into which the Inquiry has resolved itself, it has had the whole-hearted co-operation of a large and experienced staff of investigators, and the help and advice of many leading men of science to whom the subject has directly or indirectly appealed.

After examining nearly two thousand cases of death from other than natural causes, and the facts and surrounding circumstances of over two hundred separate outbreaks of disease, the Committee have arrived at the conclusion that the Strongyle worm, and the Strongyle worm alone, is the immediate *causa causans* of adult "Grouse Disease."¹

Strongyle
worm the
cause of
adult
"Grouse
Disease."

The Inquiry has not confined its energies merely to restating the theory advanced by Dr Cobbold in 1873. It has put the question to the test by proving not only that Grouse under certain specified conditions die by an over-infection of the Strongyle worm, but also that healthy birds can be artificially infected with overdoses of the worm in its larval form, and that, provided the

¹ N.B.—Coccidiosis (chap. xi.), the most common cause of mortality in Grouse chicks, can rarely be described as the direct cause of the death of adult birds.

doses are sufficiently often repeated, the bird can be done to death with all the recognised symptoms of true "Grouse Disease."

In addition to the examination of the cæca or blind guts of diseased birds the Committee have paid very close attention to the intestines of healthy birds, with the result that over 95 per cent. of the birds examined have proved to be infected with the Strongyle worm; that is to say, that almost every bird on a moor contains in its body under normal conditions the immediate cause of "Grouse Disease," and is to a greater or less extent an agent for the dissemination of that scourge.

If we admit the truth of these statements, and close perusal of the preceding chapter will make it difficult not to do so, we see at once that we have in the Grouse, not a bird free from all the ills that flesh is heir to, struck down in its thousands at no infrequent intervals when the gods are unkind, but rather an unfortunate moor-fowl, carrying in its body an inherent liability to disease which only requires certain specified conditions to develop and turn the hardiest of all game birds into a badly-feathered, rusty pinner, scarcely able to fly, and ripe for death.

What the conditions are that make this latent and endemic evil assume an epidemic or partly epidemic form is a subject which is all-important to moor-owners, and on the correct definition and diagnosis of these conditions the health of the moor directly depends.

Briefly put, we have two factors common to all epidemic diseases, the always present, occasionally harmful intruder, and the host; that is to say the Grouse, at times successfully resistant, at times pathologically affected by the nematode worm. In examining the action of these two variant factors from the point of view of the moor-manager, all that is necessary to ascertain is (1) with regard to the Strongyle—what are the predisposing causes which affect its occurrence in the Grouse's cæca, in greater or less numbers with more or less harmful consequences? And (2) with regard to the Grouse—what are the predisposing conditions that tend to raise or lower the bird's power of resistance to the ever-present evil?

If we can get a clear conception of these two sets of contributory causes we can proceed with some confidence to investigate measures put forward for the improvement of the health of moors.

Life history of the Strongyle worm. Before considering the conditions affecting the degree of infection of birds by the Strongyle worm, it is necessary to refer to the life history of the parasite itself.

As will be seen in chapter x., this portion of the investigation has afforded the Committee no little difficulty; the small size of the worm, and the fact that a great part of its existence is passed outside its host, have made it difficult to follow this parasite through all its changes of form.

The proverbial hunt for a needle in a bundle of hay is simplicity itself compared to the labour of detecting the larval nematode (so small as to be visible only under a high-power microscope) in an acre of heather. In addition to the difficulties arising from the size of the worm, the search is made more complicated by the presence of other free-living nematodes, very easily mistaken for *Trichostrongylus pergracilis*. Some of these complete the whole cycle of their life in the soil, and are never parasitic at all.

With very few exceptions every Grouse has in its body a varying number of Strongyle worms, of which the females are each capable of producing many eggs; these eggs pass from the body with the cæcal deposit, and after three days' incubation on the moor reach the larval stage. The cæcal deposit is well known to all field observers, and is readily distinguished from the hard cartouche-shaped dropping of the main intestines by its light chocolate brown, viscous appearance.

The number of the larvæ in a Grouse-dropping varies enormously, and depends directly on the degree of infestation of the bird from which it comes; in the case of heavily infected birds they may be reckoned in tens of thousands.

The larvæ during the earlier stages of their existence appear to have the power of lying dormant for an indefinite period, they are not affected by the frost; a rise of temperature will at any period raise them out of their torpid condition; excessive drought and perhaps the salt spray of the sea are the only conditions injurious to their health.

After passing through the casting of skins common to most nematode worms, and after a period generally to be reckoned in weeks, but probably never less than ten days, the larvæ assume a resistant sheath and become active young nematodes; they climb the shoots of the damp heather, and, like the East Coast fever-tick on the South African spear-grass, lie in wait for an opportunity to complete their life history by returning to their natural host—incidentally their prey.

Once the Strongyles have returned to their host the further stages of their life history follow on in rapid succession. Absorbed with the heather shoot into the crop, protected in the gizzard by the sheath-like covering from the action of

any but the sharpest grits, the encysted Strongyles pass once more into the cæcum, and on the third day reach the adult stage; the females become fertile, and three days later the myriad offspring set forth once more to infect the moor.

It is only when the adult Strongyle is found in the cæcum in large numbers that the health of the Grouse is appreciably affected. If we consider that birds may be packed in large numbers on one portion of the feeding area, for perhaps weeks at a time, herded together by stress of weather or shortage of food, that the number of Strongyles will increase by geometrical progression as the birds get more heavily infected, and therefore increasingly able to foul the moor, it is not difficult to realise, despite the countless thousands of larvæ destroyed by drought, mishap, heather-burning, etc., how the moor may become more and more tainted, until at last every shoot of heather bears the seeds of "Grouse Disease."

Equal in importance to the presence or absence of the Strongyle is the second factor, the power of resistance of the individual Grouse. The fact that the normal Grouse, in the proportion of ninety-five to five, has its cæca charged with Strongyle worms shows that, under a certain set of natural conditions, the worms are not necessarily hurtful to their host. Upset the natural balance, and this at once ceases to be the case.

This varying power of resistance of the host to parasitic or bacterial infection has long been a recognised commonplace of science.

Recent scientific investigation seems to indicate that the power of resistance varies directly with the health of the subject, and as far as the Committee's investigation goes, the Grouse appears to be no exception to the rule. A bird in full health, weight, and plumage can carry his quota of Strongyles like an alderman his wine; but once allow the vitality or weight to go below a certain recognised figure, then immediately the Strongyle worm appears to operate on the tissues of the lining of the cæca. The cæca become inflamed, the digestive process is no longer effective, the moult is delayed so that the bird loses the fresh colour of its plumage, it declines in weight, and, after a more or less protracted resistance, eventually succumbs.

Without going into the whole argument in support of this theory it is only necessary to say that the weight of the bird is the most easily recognised indication of its power of resistance to disease. That nine-tenths, if not all, of the outbreaks of "Grouse Disease" have their origin in the spring, when the food-

supply is at its shortest, and when the bird is in its lowest condition; that in early spring the cock-birds, wearied out with fighting for their nests and mates, lightened in condition and without time to feed, die in the proportion of seven or ten to one hen; whereas in late spring and early summer, when the hens are weakened after their moult, and light in weight through shortage of food during the sitting period, the relative proportions in the death-rate are reversed.¹

From the consideration of the two factors set out above, the immediate objective of the moor-owner stands out clearly—to keep the Strongyle infection at its lowest, to keep the power of resistance of the stock at its highest, and at the same time to maintain the greatest number of birds that the moor is capable of supplying with suitable food.

Successful moor management may therefore be defined as the maintenance of a margin in the power of resistance of the weakest individual Grouse, sufficient to enable it to overcome the greatest nematode infection to which the surrounding circumstances may render it liable. To put it briefly and in practical language: *Moor management is the science of distributing the stock of birds over the moor, so that at no period of the year can any area be so infected by the Strongyle worm as to make it a source of danger to the least well-nourished bird (that is, to the bird of the lightest weight) on that area.*

Definition
of moor
manage-
ment.

In considering this definition it is important to realise not only the main factors, but also the contributory causes which produce them, (a) the power of resistance of the Grouse, which varies directly with diet, moult and seasonal conditions, (b) the liability to infection, which varies with the number of larval nematodes on any given feeding-ground. These contributory causes in turn depend on the number of birds on that area, the number of nematode eggs deposited in each caecal dropping, and the length of time that the stock has been congested on any portion of the ground.

It must be clearly understood that the Committee do not wish to lay down that "Grouse Disease" is dependent on any fixed number of Strongyles in the caecal intestines, or that any fixed standard of power of resistance guarantees immunity from the disease, but rather that the epidemic depends on the relation

¹ N.B.—Investigation in the Frimley area has shown that light birds and birds not in good plumage die more easily from artificial infections of nematode worms, and measurements go to show that light and weakly birds of one year, without sufficient strength to feed themselves at the time of stress in winter and autumn, are the piners and diseased birds of the year following. *Vide* chap. xxi. pp. 469-470

between the amount of infection and the power of combating the same. That is to say, that the nematode infection which would be fatal to the weak bird might conceivably be the normal burden of the strong Grouse; and that the same bird might carry with ease in autumn—when well nourished and fully feathered—the number of Strongyle worms to which he would succumb in spring when light in weight and short of food. If we realise this theory in its entirety we shall find ourselves on vantage ground, from which the many and apparently contending aspects of “Grouse Disease,” and the numerous hypotheses based thereon, can be readily explained.

CERTAIN THEORIES OF DISEASE HELD BY SPORTSMEN AND FIELD OBSERVERS.

Theories of
“Grouse
Disease”
(1) Frosted
heather.

First Theory.—A very common theory, especially on the west coast of England and Scotland, is that frost is the cause of “Grouse Disease.” This theory is usually stated in the form—that “the frost of early spring browns the heather, birds eat the heather and die of indigestion.” This is a very good example of an incorrect deduction drawn from properly observed natural phenomena, and of the ease with which secondary causes are confused with primary ones. It is quite incorrect to say that frost in spring is the immediate cause of “Grouse Disease,” for the very excellent reason that of nearly two thousand crops examined by the Committee not one single crop has been found to contain a shoot of brown or frost-dried heather. It is, however, correct to say that when frost comes in late spring, or when the cold east winds brown the young shoots, the area of ground on which the birds can feed is reduced, and there may be therefore both a lowering of the Grouse vitality through a shortage of the food-supply, and an increased danger of infection by the Strongyle worm, through the congestion of the birds upon a small area of feeding-ground. At this season also large areas on some moors begin to show the “burned” and “foxy red” appearance which is caused by the attacks of the heather beetle. The old stick heather, ragged and sparse, is of little use for food. It is only in the thick six- to fifteen-year-old heather that green shoots can be found under the browned tops.¹ As will be shown later, on a badly-burned moor this may mean a very great curtailment

¹ See chap. xix. p. 422.

of the food-yield of the moor; greater perhaps than the health of the weaker birds will stand.

Second Theory.—It is stated that disease comes every seven years: that it is a recognised order of creation, and that no effective steps can be taken to alter the periodicity of its recurrence. This theory, like the preceding frost theory, is quite beside the point. In the first place, “Grouse Disease” does not occur on any moor in the regular order of once in seven years. The examination of some hundreds of Grouse records show that the disease occurs, on those moors which are liable to the epidemic, at irregular intervals of three to eight years.

(2) Periodic outbreaks unavoidable.

The ordinary sequence of events is, one year of disease, one or two years of recovery, two or three average seasons, one or occasionally two bumper years, followed by disease in the following spring. Disease after a record year is due partly to a heavy Strongyle infection in the winter months, resulting from an overstock at a time when the birds are packed together on the lower portions of the moor, partly also to the Grouse's decreased power of resistance arising from a heavier stock without a corresponding increase of the food-supply. As has been already pointed out this food shortage is most marked in spring, and the outbreak of the disease accordingly occurs at that time.

Third Theory: Klein's Disease.—The third theory, associated with what is commonly called Klein's disease, is that the mortality can assume two forms, the first or epidemic form (pneumo-enteritis), which sweeps the moor, and in which the birds are said to die in plump condition, fully feathered; the other a lingering disease in which birds waste away and die only after loss of plumage and weight. The Committee have paid very close attention to Klein's disease, and the remarks on p. 200 should be read. It should be noted that in all the outbreaks investigated not one single case was found of birds dying in good condition, *i.e.*, at normal weight.

(3) Two forms of disease.

On seventeen different occasions during the course of the Committee's investigations keepers have reported birds dying plump and

fully feathered; in every case the spring balance has indicated that the birds referred to were below the normal weight, and visceral examination has shown that the cæca were charged with Strongyle worms.

Piners are found in every outbreak of disease, and experience on the Frimley observation area, as well as research in the field, goes to show that there are always some birds wholly or partly able to combat the disease, owing either to their previous good condition of health, or to their being less heavily infected by the Strongyle worm.

Fourth Theory.—The fourth theory put forward is that when birds die of disease on lightly-stocked moors it is impossible that they should die of shortage of food or by parasitic infection, and that therefore midges or gnats must be the cause of death. This theory is not supported by any ascertainable facts or data, and, as far as examination of the blood goes, there is strangely little evidence in its favour.

(4) Midges
or gnats.

Small stock
does not
secure
immunity.

It cannot be admitted that a shortage of stock on a moor is necessarily a guarantee of immunity from infection by the Strongyle worm, although it may lessen the risk of such infection. It will be shown later that moors in Yorkshire, which one hundred years ago were unable to carry three hundred brace to ten thousand acres without a certainty of disease, have by careful burning been made to carry ten times that stock without risk.

Infection of a light stock can be brought about in various ways:—

Congestion
during time
of snow.

(1) If, in a hard winter, the birds are driven by snow off their own ground and congested on a small feeding-area for a long enough time for the larval nematode to go through its changes and infect the heather, the birds may become so charged with Strongyle that they die as soon as they return to their own ground, however lightly stocked that ground may be.

There are very few owners of high-lying moors who have not heard the remark: "The birds were quite healthy before the last winter storm; as soon as they returned to the high ground they began to die."

(2) "Grouse Disease" occasionally appears the second and third year after a severe epidemic, especially on wet, badly-drained moors, and this notwithstanding the small stock that may have survived the first outbreak. As has been shown in chapter ^{After-effects of severe epidemic.} x,¹ the Strongyle worm flourishes best in damp surroundings, and it is possible that on a wet moor a smaller quantity of ova may be sufficient to cause fatal infection.

(3) On the west coast of Scotland a very light stock sometimes contracts the disease. West coast heather is, as a rule, of ranker growth and more open habit than what is found on the east coast; it is therefore more liable to be scorched by ^{Shortage of food.} the frost and cold winds of early spring. The food-supply in consequence is apt to become so short that the normal quota of Strongyle worms are enabled to become actively pathogenic without the aid of further and outside infection.

Fifth Theory.—Another theory put forward is that a hard winter affects the health of a moor. This theory takes two forms. First, ^{(5) Hard winters.} that a hard winter makes for a healthy stock, and secondly, that a hard winter causes disease in the following spring.

These theories are mutually destructive, but, paradoxical as it may appear, both are conceived on a certain basis of truth. A hard winter tends to kill off sickly birds, to shift the stock and to mix the breed; snow lying on the heather till far into the spring protects it from larval infection during the critical months of February and March, and so ensures a fresh, untainted food-supply in April and early May; lastly, heavy snow followed by floods tends to wash the moor clear of Strongyle larvæ; all these are factors which benefit the moor.

On the other hand, a hard winter may do incalculable harm if the birds are driven off the whole of the hill-ground, and massed for several weeks on a small area of feeding-ground. The winter storms, especially in the Highlands, drive birds off great tracts of heather land, with the result that when the food is at its shortest the local feeding-area is reduced sometimes to a half, in some

¹ Chap. x. p. 226.

cases to a tenth, of its normal size. The migration of birds is a question that has only recently been studied, and some very remarkable facts have been brought out as to the extent and length of time that birds desert the high ground.¹

(6) Feeding on corn. *Sixth Theory: Corn Theory.*—This theory suggests that by eating corn in the stook birds are seriously affected in health, and die of disease in the year following.

This is another example of faulty deduction from correctly observed natural phenomena. The fact that birds go off the moor in October to eat corn on the low ground usually means that there is not a sufficient natural food-supply on the moor.

If the birds are short of food in autumn and early winter it is quite certain that they will be still shorter of food in the spring when the carrying capacity of the moor is at its lowest, and it is easy to see how the birds will in consequence become liable to the hurtful influences of the Strongyle worm.

It is not necessary to go into any of the other theories of "Grouse Disease" examined by the Committee. The majority appear to be based on a misinterpretation of natural phenomena, and in most cases confusion has resulted from mistaking the predisposing conditions for the immediate causes. All the theories on the subject fall into line with the solution put forward by the Committee, that the immediate cause of "Grouse Disease" among adult Grouse is the Strongyle worm, and that there is an intimate relationship between the power of resistance of the stock and the degree of infection required to affect the birds injuriously.

Remedial measures proposed. The next question that has to be considered is whether there is any proof that this relationship can be artificially controlled. Can it be shown that more birds can be carried on a moor if they are well distributed, and if their vitality and weight are raised by an increased supply of food at all times of the year? The answer to this is undoubtedly Yes! and the four following examples are put forward to show what results have been obtained on well-managed moors.

¹ *Vide* chap. iii. pp. 25 *et seq.*

Bolton Abbey Moors, Yorkshire.

These are high well-burned moors with good grit; they are well watered and considerable attention has been paid to draining; the patches burned on the moors every year are very large; they have probably not always been so well burned as they are to-day, and the older heather takes three or more years to spring from seed after burning. The average annual rainfall is about 38 inches. The record given below is a very remarkable one, extending as it does over a century. The following points should be noted:—

- (1) That the yield of Grouse has increased from two hundred to over three thousand brace.
- (2) That for the first twenty years any year in which over three hundred brace was killed was invariably followed by disease, that is to say, that the same land which now carries three thousand brace with safety, could not then stand a bag of more than two hundred brace without risk from disease.
- (3) The difference is very marked in the time required for the moors to recover from the epidemic under the new and old conditions. When the moors were badly burned it used to take three to four years to get over a bad outbreak of disease; in the last two outbreaks the season following the attack has given an average yield.

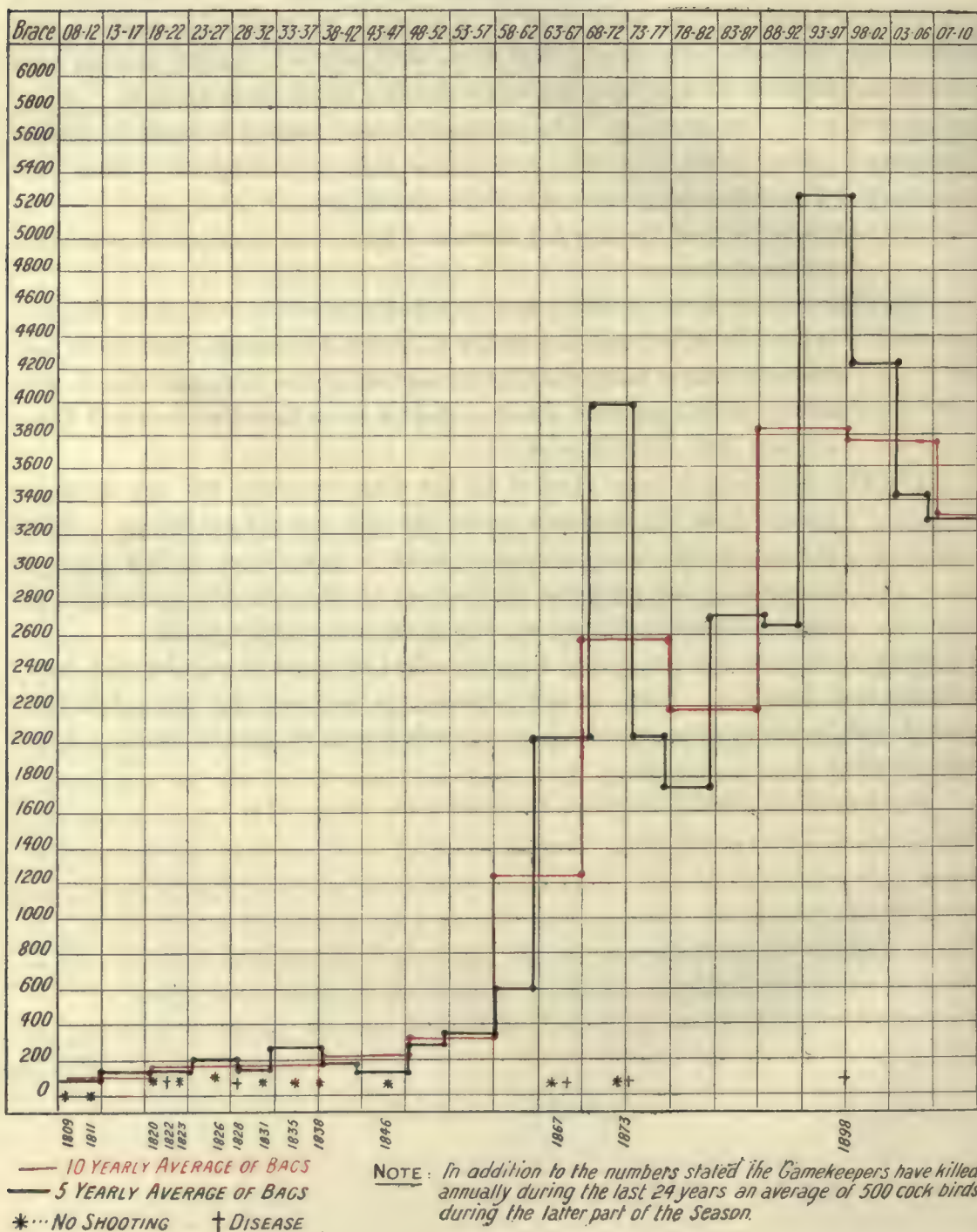
These moors are still improving from the effect of years of regular and heavy burning and draining. There is every reason to suppose the rate of heather growth will increase, thus affording an extended area of ground bearing a full crop of food.

An analysis of results is given in chart form on p. 384.

BOLTON ABBEY MOORS NEAR SKIPTON IN YORKSHIRE.

14,000 ACRES

ANALYSIS OF BAGS



Broomhead Moor, Yorkshire.

This is a very remarkable moor. It has been well cared for for over forty years ; it is now probably one of the best, if not the best burned moor in England or Scotland, with the result that it has not only the thickest but also the quickest growing heather that the Committee have seen anywhere.

There are not twenty square yards of stick heather on any portion of the ground ; there is a *larger* proportion of six- to twelve-year-old heather than on any moor the Committee have investigated, a bigger stock of birds is carried to the acre, and disease has not occurred for over thirty years.

In examining the Game Records the following points are of importance :—

- (1) The steady growth of bags from two hundred brace before 1870 with disease recurrent every few years, up to two thousand seven hundred brace per annum with no danger from disease.
- (2) In the last decade there appears to be a slight set-back, but this is more apparent than real, and unsuitable weather in the shooting season is largely responsible.
- (3) There is now a larger stock on the ground than ever, and the owner with forty and the keeper with fifty-one years' experience of the moor are agreed that the maximum yield has not yet been reached.

The points about this moor that are specially noteworthy to moor-managers are that :—

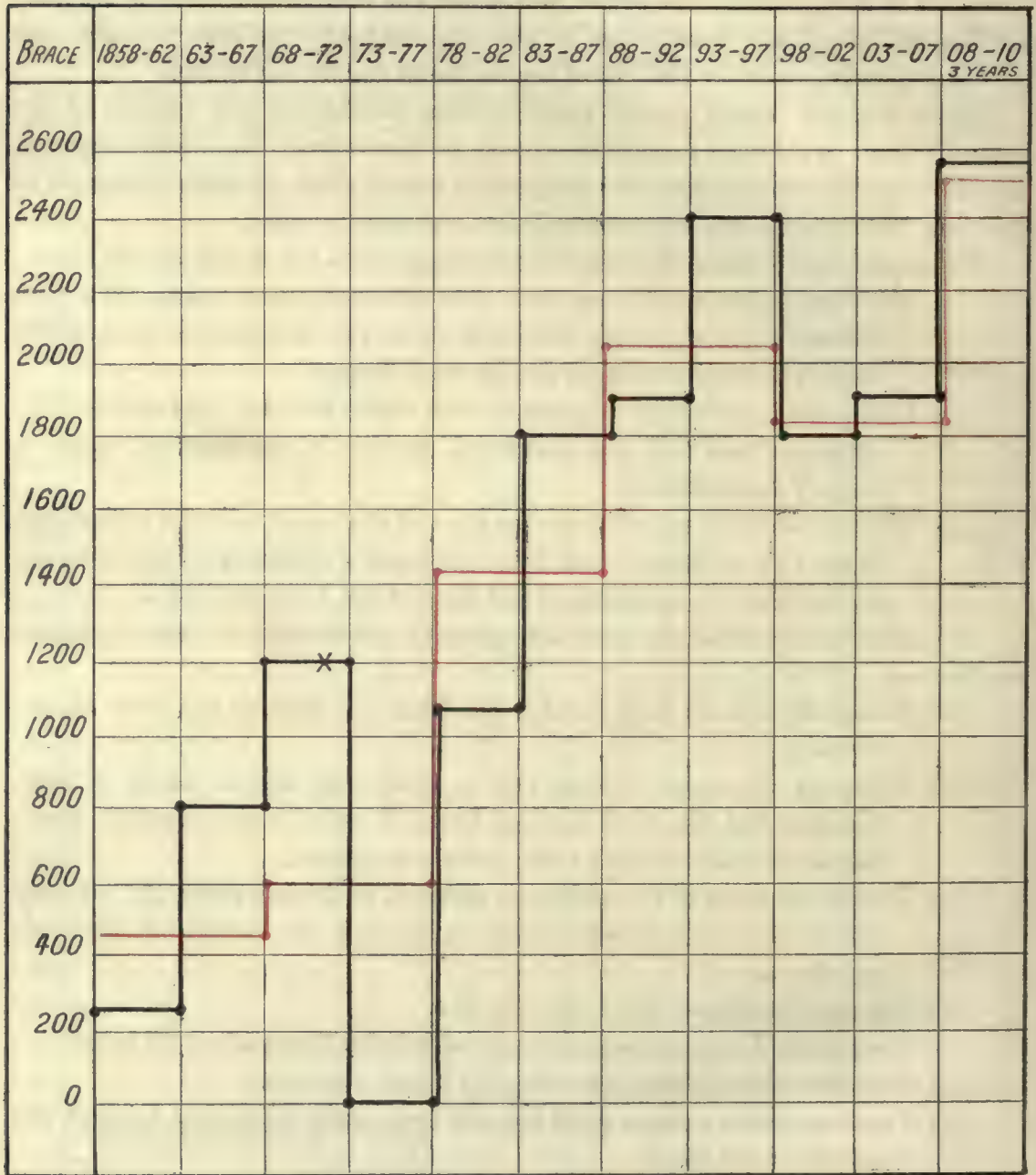
- (1) Though there is no long heather the birds are kept on the moor all the winter.
- (2) Although the moor is relatively a small one, and is burnt in large patches, yet the total acreage burnt is only, with difficulty, maintained at one-twelfth of the moor per annum.
- (3) The management of the stock and methods of driving (*vide* Mr Wilson's note)¹ have undoubtedly much to do with the health of the birds on the moor.
- (4) The moor is all over the 1,000 feet line.
- (5) The climate is dry, the average annual rainfall being about 30 inches.
- (6) Beautiful white quartz grit is found all over the moor.
- (7) There are about a dozen good springs, and a deep burn runs through the centre of the moor.

¹ *Vide* chap. xxi. p. 480.

BROOMHEAD MOOR NEAR SHEFFIELD IN YORKSHIRE

4,000 ACRES

ANALYSIS OF BAGS



X NO SHOOTING

— 10 YEARLY AVERAGE

— 5 YEARLY AVERAGE

A chart is given on p. 386 showing the gradual improvement in results which has followed improved methods of management. It should be mentioned that the steady increase in the stock commenced about 1872, and that it was just before that date that close and constant heather-burning was first introduced.

Carron Moor, Morayshire.

A moor of about 3,000 acres, of which about 1,000 are flow ground, and the rest heather. The altitude ranges from 700 to 1,300 feet. Previous to 1897 the heather-burning had been neglected, in many parts it had grown to a height of 3 feet or more; since that year the burning has been most carefully and thoroughly done, when possible. The heather all over the moor should continue to improve. The hill has only been regularly burnt for the last fourteen years, and during some of that time, owing to bad weather, little or no heather could be burnt. A considerable quantity of old heather still remains to be burnt, and much that has been burnt has not yet reached the most valuable stage. Good grit is abundant, and great attention has been paid to drainage. A moderate stock of sheep is carried on the ground.

In 1910 the experiment was tried of introducing an artificial water-supply to the drier parts of the ground by means of dew pans. The results appear to have fully justified expectations; in one case it was observed that five coveys were hatched in the immediate vicinity of a dew pan, where there were no young birds before. The results are conclusive so far as they go, but the experiment has not been continued long enough to admit of absolute certainty.

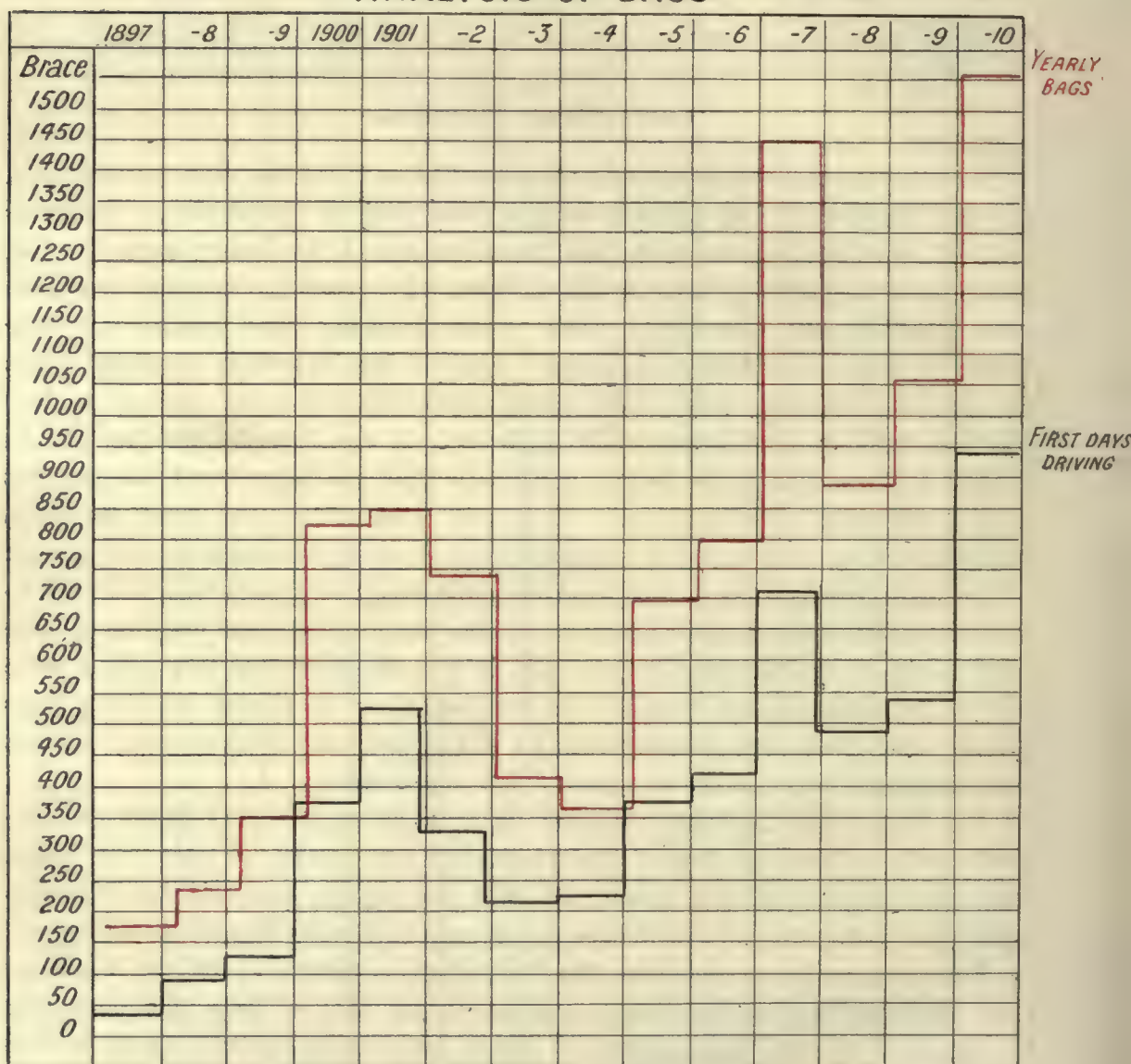
The years 1907-1908-1909 yielded an average bag of 1,114 brace, as compared with an average bag of the years 1897-1898-1899, of only 241 brace, showing an increase of 873 brace. In 1910 the bag up to September 20th was upwards of 1,800 brace. No disease has occurred since this improvement began.

From the evidence available, the Committee is satisfied that the whole of these birds are bred on the moor, and the theory that so large a bag can only be obtained by the immigration of birds from neighbouring moors is not supported by the evidence. The progress of the stock is carefully watched from the date of hatching to the commencement of the shooting season, and it is always found that the total bag corresponds to the prospects at the nesting season; there are no berries on the ground to attract neighbouring

CARRON MOOR MORAYSHIRE

3,000 ACRES

ANALYSIS OF BAGS



	1st days driving
1897.....	44 BRACE
1898.....	93 "
1899.....	128 "
1900.....	373½ "
1901.....	420 "
1902.....	326 "
1903.....	211½ "

	Yearly Bags
1897.....	158 BRACE
1898.....	223 "
1899.....	341½ "
1900.....	804 "
1901.....	850 "
1902.....	745 "
1903.....	403½ "

	1st days driving
1904.....	215 BRACE
1905.....	378 "
1906.....	414 "
1907.....	715 "
1908.....	470½ "
1909.....	548 "
1910.....	946 "

	Yearly Bags
1904.....	350½ BRACE
1905.....	686½ "
1906.....	778 "
1907.....	1439½ "
1908.....	861 "
1909.....	1043½ "
1910.....	1500 "

birds, and the first day's driving always takes place before any of the surrounding moors are driven.

Towards the end of the season there is often an immigration of birds from other moors; but these visitors arrive after shooting has ceased for the season, with the exception of the gamekeeper's annual crusade against old cocks.

The whole stock has been known to leave the moor in time of heavy snow, and to remain away till the snow has disappeared; but such migrations have not been found to affect the number of birds on the ground at the next nesting season.

The owner of the moor has drawn the following deductions from the foregoing facts :—

- (1) That it is possible, by improving the heather, to raise the permanent stock of Grouse that a moor can carry without fear of disease developing locally, *i.e.*, among the home stock of Grouse.
- (2) That drainage is very beneficial.
- (3) That an abundant supply of good grit is essential.
- (4) That Grouse driving is largely responsible for the increase.
- (5) That the limit has not necessarily been reached.
- (6) That the introduction of an artificial supply of water may be beneficial in a dry season or on the drier parts of the moor.

Cawdor Moor.

A very fine moor not yet fully developed or arrived at its full carrying power, with good young heather. The following points in the record should be noted :—

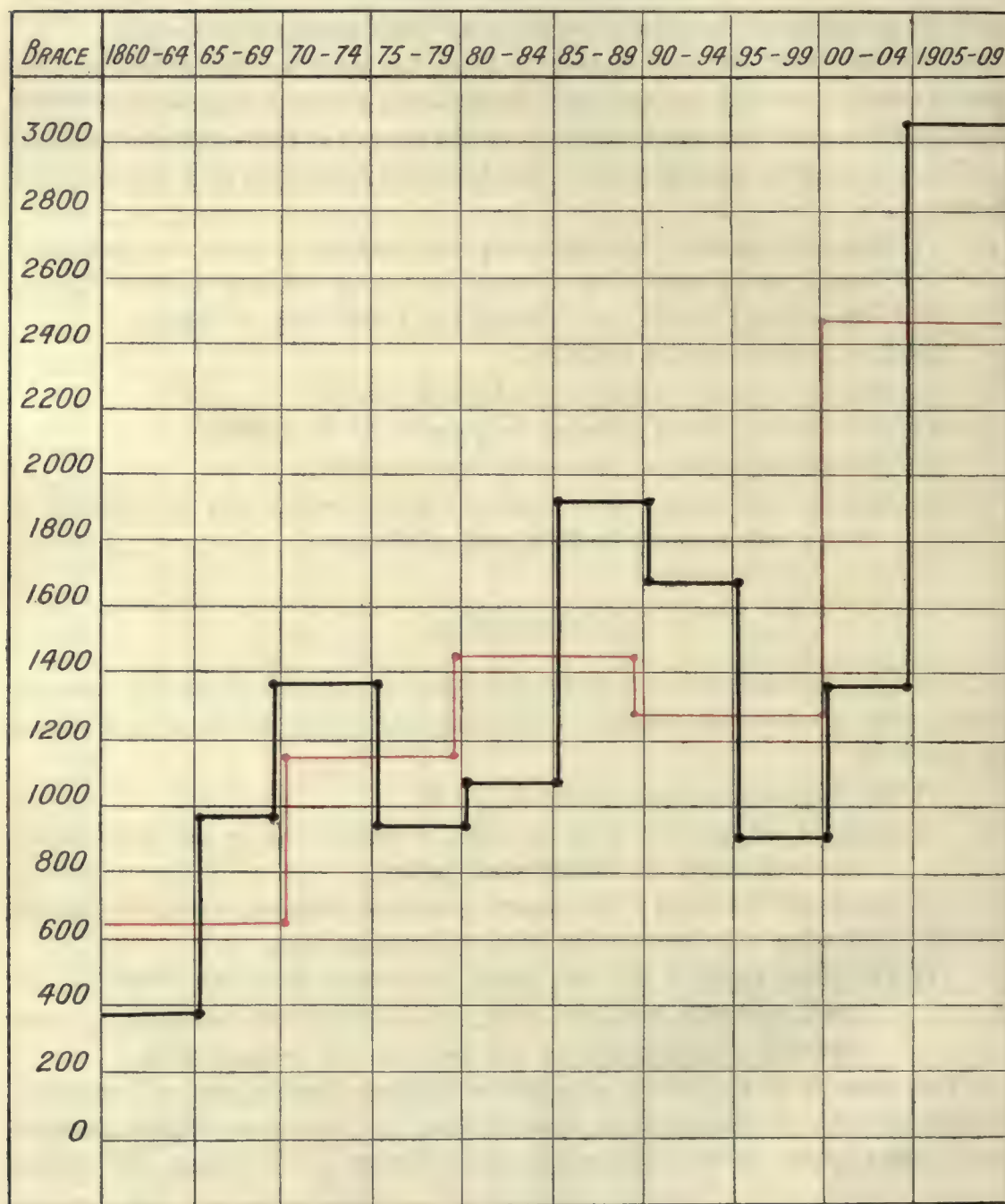
- (1) The improvement in each decade.
- (2) A slight set-back in 1890 to 1900, probably due to the moor being less well cared for during that period.
- (3) The period 1900 to 1910 shows a marked advance, owing to regular driving and improved methods of management.
- (4) The time required for the moor to recover from the effect of the 1907 epidemic was one year; on all previous occasions it took upwards of four years to get back to the average yield.

This moor is in the centre of a Grouse-bearing district, and will probably always be liable to disease from overcrowding by birds from higher and less well-burnt moors in late winter and early spring. This danger will remain

CAWDOR MOOR - NAIRNSHIRE

30,000 ACRES

ANALYSIS OF BAGS

NOTE. THE BAG IN 1910 UP TO 9TH OCTOBER WAS 6513 BRACE.

— 5 YEARLY AVERAGE

until some system is adopted for the proprietors taking joint action to regulate the stock in good Grouse years.

From the examples that have been given four deductions can be made :—

- (1) That it is possible by careful management to raise the permanent stock of Grouse on a moor, and do so without increasing the danger of infection beyond the power of resistance of the individual bird.
- (2) That during the various stages or periods of development of the carrying capacity of the moor there is a corresponding limit of stock which it is dangerous to come up to, and fatal to exceed.
- (3) That as far as yet ascertained the limit has not been arrived at on any moor beyond which a permanent increase of healthy stock is not possible by improved moor management.
- (4) That, though many moors by their proximity to less well-managed moors, and through the difficulty of getting the stock killed in a good year, immigration, abnormal seasonal conditions, etc., cannot entirely escape the ravages of disease, yet there is every reason to believe that the disease is both rarer, less hurtful in its incidence, and quicker to pass away on the well-managed than on the badly-burnt moors.

CHAPTER XVIII

HEATHER - BURNING

By Lord Lovat

THE student of the heather-burning question will be struck, from the very outset of his inquiry, by the curious fact that while all parties are agreed that there is the closest possible relation between the state of the heather on any given moor and the health of the birds on that moor, there is the greatest divergence of opinion, not only as to what are the best methods of burning, but even as to what are the special characteristics of a really well-burned moor.

Variety of
opinions as
to heather-
burning.

The vexed question of the relative values of autumn- and spring-burning, the percentage of a moor that it is advisable to burn in any given year, the effect on the heather of the presence or absence of sheep, the limit of sheep stock desirable, the proportion of long heather to be left for spring feeding or cover, the management of the steep slopes for winter feeding, the methods of burning—patches, blocks or strips—and the treatment of the various descriptions of moorland, all give scope for a much greater variety of opinion than the difference of local conditions appears to justify.

In the previous chapter, the findings of the Grouse Committee have been discussed in relation to the various ideas which have been put forward as to the causes of disease; in the present chapter it is proposed to discuss the practical steps that must be taken :—

- (a) To raise the power of resistance of the Grouse ;
- (b) To lessen the risk of nematode and coccidian infection ; and
- (c) To compare these with the methods which have in the past been evolved from *à priori* reasoning.

With these objects in view it is intended, in the first place, to trace briefly the history of moor management in the last century, to show how blind but

intelligent experiment has slowly been working its way towards comparative hygienic success ; to see where methods have failed through incorrect deductions from observations of natural phenomena ; to indicate broad lines of moor management in accordance with our present standard of knowledge ; and lastly to lay down lines on which further experiments can be tried with reasonable prospects of success.

In the early days of Grouse shooting, when shooting rents were low or non-existent, and the Grouse was an appanage of the sheep farm, not the main rent producer of a hill property, the moorland in the majority of cases was burned by the farmer and his shepherds. The methods used were rough and ready, but effective. The object, as set out in the tack or lease, was to burn one-tenth of the moor ; the driest and most windy days were chosen, and, provided the hirsels were burned approximately in the authorised proportions, the matter of a few acres more or less in a single burning was not considered of much importance.

History of
heather-
burning.

Heather
formerly
burned by
sheep
farmers.

Judging from occasional bags recorded it is probable that during this period the actual stock of Grouse throughout the country was often very considerable though the stocks were seldom fully shot and the recorded bags are so scanty that an exact comparison with the results of the present day is impossible.

In the middle of the last century in England, and in Scotland a few years later, railway facilities, improvement in guns, increase of wealth, and, more than anything else, fashion, made the sporting value of the Grouse moor gradually approach the grazing value of the farm.

The Grouse, up to then the occasional victim of the landlord and his friends, or of the poacher for the pot, became all at once a saleable article, for which there was, and has been since, an ever-increasing demand. The moor-owner was quick to realise the enhanced possibilities of his property, keepers were appointed to even the smallest acreage of heathland, and the rights of burning the moor were transferred from the shepherd to the keeper, under the mistaken idea that the policy of burning to benefit Grouse, not sheep, would at once increase the yield of birds.

Heather-
burning
transferred
to game-
keepers.

It is a curious fact that, while the average man can predict with some degree of certainty the immediate result of any change in the existing order of things, the correct calculation of even secondary consequences requires the attention of brains of a very different calibre. When the landlords in their wisdom appointed the keeper to the rôle of moor-burner they achieved their

immediate aim—better cover for shooting over dogs; but they gained also a second and not less noteworthy result, a drop both in the average bag of Grouse, and in the grazing value of the hill-ground, a thing neither foreseen nor in any way desired.

Founded on latter-day experience the reason for this is not far to seek. In the dogging days the long heather was the ideal. “Keepers’ delight,” applied to 3-foot heather, is still a recognised and but too often well justified term. The keeper, acting up to his lights and wishing to show the best sport on the Twelfth, not only stopped the shepherd from burning big stretches of heather, but stopped him from burning the heather at all. In books of sport in the year 1863 places are mentioned—as splendid Grouse ground—“fifteen hundred acres of heather without a single break!” This method of heather culture was admirable for approaching wild birds; in these jungles a covey once settled could be massacred at ease with “snap-hance” or breech-loader. Unfortunately, the change of methods was not equally satisfactory with regard to the health of the moor, and a very rude awakening was not far distant.

A few lucky seasons, with a heavy crop of heather seed for food in winter and early ripening shoots in spring, gave in certain favoured districts an increase of bags by improving the conditions for approaching the birds; then a cold summer followed by a winter with late spring frosts, and a seasonal shortage of food intensified by an overplus of old stick heather, led to the inevitable result—a general outbreak of disease.

As early as 1857 there were reports of heather on certain moors “man high”—by the sixties the whole effect of the shepherds’ burning had passed away, and in many districts where the non-burning practice was at its height, not only were there few birds and disease frequently recurrent, but the graziers’ complaint became more and more common—that there was not enough young heather and grass to feed the sheep-stock. At this period the relations between sporting tenants and sheep-farmers became so strained that big sheep-farmers, then a well-to-do class, used in many districts to rent the shooting as well as the grazing of their holdings, and so get the control of heather-burning into their own hands.

In 1871 and 1873 the Game Laws Commission investigated the relations of the sporting and farming interests, and some very interesting facts were elicited. Not the least important of these facts was the similarity of heather conditions required for sheep and for Grouse. This was brought out by the evidence of farmers

Outbreaks
of “Grouse
Disease.”

Failure of
grazing.

who had leased the sporting rights of their farms, and who spoke of doubling and trebling the bag of Grouse by burning tracts of ground in order to get the land back into the proper rotation for sheep, viz., one-tenth of the moor burned per annum.

The reports of these and other successes obtained by heavy burning were not long in being spread abroad. Partly from increase of knowledge, and partly to satisfy the sheep interest, more intelligent methods were pursued. On many estates the principle was adopted—"The shepherds light the fire, the keepers put it out." As a principle rather than as a practical usage this is not far from the ideal. The shepherd wants the acreage burned for food, the keeper wishes the patch or strip method maintained for the segregation of birds.

Matters in the early seventies were thus proceeding through the usual course of friction and inquiry towards mutual understanding and settlement, when in 1872 and 1873 the great disease year occurred.¹

Just as 1881, by the introduction of the Ground Game Act, may be described as the Jena of the rabbit, so for a very different reason 1872 and 1873 may be said to be the Austerlitz of the Grouse. From end to end of the Grouse area an epidemic created unparalleled destruction; authorities realised that old methods must give place to new ones, and from that date the intelligent management of moors may be said to have commenced.

Broadly speaking, we may divide the history of heather-burning into three periods, not always synchronous, but through which the majority of moors have passed at one time or another.

1800 to 1850, when the heather was burned by the shepherds in wide tracts, and one-tenth of the moor was fired every year without any attempt at scientific burning. During this period shooting rents were low. Large blocks of land were hired in Scotland for as many sovereigns as they now fetch hundreds of pounds. The frequently quoted example of the sporting rights of the Island of Lewis, hired by Lord Malmesbury for a period of years for £25 per annum, is a case in point. At this time few moors were rented in England, and although Grouse driving had just begun in Yorkshire the results generally were not great, and the flint-lock, contemporary writers tell us, still had its devotees in the firing line! Mr Snowie of Inverness was the only shooting agent for Scotland, and the names of moors for hire could be contained on a single sheet of foolscap.

1850 to 1873 marks the transition period of heather-burning. Moors generally

¹ *Vide* vol. ii. Appendix I.

were taken into the hands of owners and shooting tenants, the patch method of burning came into fashion, and the proportion burned, as far as ^{2nd Period} records show, dropped from one-tenth to one-hundredth part of the moor burned per annum. ^{1850 to 1873.}

In this period great strides were made towards fitting out shootings with lodges, approach roads, and other conveniences. Large sums were paid out in the wilder and poorer districts, and a great deal of employment was given.

Moors were let for sheep and Grouse at about the same figure. It is instructive to note that to-day on many of the same moors sporting rents represent five, in cases ten times the value of the grazing rents.

The third period begins with the years of disaster 1872 and 1873, which were followed by four years of recovery and very restricted bags. These lean years were the immediate cause of the study of Grouse pathology. The investigation has continued more or less ever since, and after passing through the vicissitudes customary to research in a new field, has culminated in the comparatively extensive knowledge of the present day. ^{3rd Period} ^{1873 to 1910.}

Notwithstanding the fact that Cobbold had indicated in 1873 that the cause of the great outbreak was the Strongyle worm, the first move towards an improved system of management was not in the right direction. The moors had been indifferently burned so long that in order to catch up the rotation, recourse should have been had to big fires rather than to the patch or strip system of burning. This, however, was not realised.

Many land-owners, seeing that "patch-burned" moors were less affected by the disease than moors on which no heather had been burned, jumped to the conclusion that it was the smallness of size of the individual patch, and not the total area of the burning that was all-important. This belief ^{Burning in} ^{small} ^{patches} ^{introduced.} is prevalent in many localities to-day, and it is no exaggeration to say that to this error, more than to any other cause, is due the persistent recurrence of disease.

From the foregoing history of past failures, and the knowledge scientific investigation has given us, we can proceed to lay down with some ^{Conclu-} ^{sions.} approach to certainty the following rules of heather-burning, and the reasons on which they are based:—

- (1) That, in order to maintain the vitality and therefore the power of resistance of the Grouse, the moor must be so burned as to keep the food-supply at its highest.

- (2) That the early spring food-supply is the index of the carrying capacity of a moor, and that therefore heather-burning must be so ordered as to insure the maximum yield of food in February, March, April, and May.
- (3) That the patch or strip method of burning must as far as possible be pursued in order to segregate the birds, and thereby lessen the risk of infection by the Strongyle worm and the Coccidium.

In discussing the question of burning for food two difficulties at once arise :—

- (1) That of persuading the average moor-owner that by burning small patches with a small staff he cannot possibly get over his moor.
- (2) That of persuading him that at any time of the year the birds can be short of food, or that there is any real difference in the heather supply on well and on badly burned moors.

To convince him of these facts it is necessary to go into figures, and those set out below may be taken as a reasonably accurate statement of conditions that obtain on many average if not model moors.

Proof of
foregoing
theories.

On the ordinary 5,000 to 6,000 acre moor in England, and the corresponding 10,000 acre moor in Scotland, on which one thousand to one thousand five hundred brace are killed in a good average year, and on which two keepers and one or more watchers are maintained, the landlord thinks he is doing all that can be expected of him if, in addition to the keepers, six to eight extra hands are employed in spring to burn the moor.

Estimate of
area
burned on
average
moor.

Speaking generally, after a careful investigation of east and west coast conditions, of high and low moors, a good spring-burning season will give an average of ten whole days or twenty half days on which the hill can be fired. Taking into consideration dry and windy weather when the fire goes well but requires great control, and wetter conditions or less wind when the fire does not "run" so fast and may be managed by a couple of men, it may be calculated that on an average each keeper, dividing his gang to the best advantage (each gang consisting of not less than two parties), will not burn more than thirty, or at the very outside forty patches or strips in a full working day. That is to say, if the small patch or narrow strip method of burning is followed (*i.e.*, burning in

areas of from one-eighth to half an acre), the two keepers and their parties will burn 20 acres a day, or a total of 200 acres of the moor in a year.

Those who have not had a practical experience of heather-burning are apt to hold exaggerated ideas as to the amount of work that can be done in a single day's burning. It is only when facts and figures are subjected to a careful scrutiny, and the amount both of the day's work and the season's results are thoroughly gone into, that the smallness of the area burned becomes apparent. If we admit this contention to be correct, a little simple arithmetic will show that 200 acres on 6,000 acres of moorland is one-thirtieth of the total area, that is to say that, if the heather is regularly fired in rotation it will be thirty years, or in the case of the 10,000 acre moor fifty years old before it comes to its turn for burning.

If we consider that every year is not a good burning year, and that on many moors on the west coast a good burning year occurs only once in three years, that some districts suffer from fogs, "haars," and mist; that others get so dried up after a continuance of east wind that it is dangerous to burn at all; that in Scotland the high ground in a late spring is covered with snow until the end of March; that there are the additional difficulties of suddenly rising winds, late dews, and of getting men away from their holdings, etc., it will be easily seen that a moor may go for a series of years with only one-sixtieth or one-hundredth part of its total area burned, and that instead of catching up the heather rotation in force when the sheep-farmer was responsible for maintaining it, many moors are steadily going back in their yield of young heather, and therefore in their power of maintaining a healthy stock of Grouse.

The second difficulty, viz., of persuading the moor-owner that his birds may be short of food, is not less great. Many proprietors only see their moors in August—every head of heather in bloom and green shoots on every stem. He sees sheep grazing at the rate of one to the acre. It is very difficult to persuade him that at certain seasons there may not be enough food for at least an equal number of Grouse.

Let it be at once admitted that through the summer and autumn, even on the worst moors, there is abundance of food; but then at that time, except for a previous infection, Grouse do not die. Let the doubter visit the moor in March, when the heather seed has fallen from the pod, when the young heather up to four and six years old is frosted a clarety red or brown colour, when the old stick heather sparsely distributed and bare of side shoots does not carry a

"canopy" with which to keep out the withering effect of the cold winds and frost, and he will find a very different state of affairs. Careful examination will show that the close-growing six- to fifteen-year-old heather with a thick matted covering affords the only feeding at this time of year, and that even here the shoots are green, not at the top, but half way down the stem, where they are protected from the cold.

It is at this time that the real test of moor management is seen, and a little careful study will prove to demonstration certain facts not found in the philosophy of the "small patch" enthusiast. Granted the premises set out above, it follows that, if the moor is being worked on a hundred years' rotation, the total amount of spring-feeding heather, that is to say, the amount that lies between six and fifteen years of age, is roughly 9 per cent. of the total area of the moor. If the moor is burned on a fifty years' rotation, which is the rotation of the majority of moors to-day, the amount is 18 per cent. of the total area. If, however, the heather is burned on a fifteen years' rotation, the rotation the Committee advise, the amount of edible heather represents nine years out of a total of fifteen, *i.e.*, 60 per cent. of the total acreage of the moor. That is to say, if we admit the early spring months to be the critical time in the life history of the Grouse—no great admission seeing that it is in spring that disease invariably appears—we shall realise that a well-burned moor can carry seven and a half times the stock of the moor burned on a hundred years' rotation, and nearly four times as much as that of the average moderately burned moor.

These figures may possibly be challenged; but with regard to the area burned the proof is perfectly simple. Employ a surveyor to measure up the patches of a strip or patch-burned moor, burned in 1910—a very good burning year—compare the acreage with the total area; the result will astonish many landlords who habitually boast that they burn one-tenth of their moor every year.

It will perhaps be argued that the six- to fifteen-year heather is not the only spring feed, that even the stout stick heather will present occasional green shoots, and therefore afford some small measure of sustenance to the Grouse in the spring-time. This is true, and it is a fact that, *faute de mieux*, Grouse are able to exist on an unburned moor. It must, however, be remembered that they require probably twice or three times as much of the sapless, partly dried-up heather of April as they do of the more succulent shoots of summer and autumn. The weights of crop contents show that

The test of
moor
manage-
ment.

More food
required in
winter.

late winter and early spring up to two hundred and fifty grains of heather are found in the average afternoon crop as against fifty grains at any other time of the year. It is therefore reasonable to say that as the Grouse have to increase the amount of their food they will naturally go to those places where edible *Calluna* is most readily obtained, and thus by congestion of the stock on a small area will not only over-crop the food there, but also, as will be shown later, will be exposed to an increase of infection by the nematode worm and by the Coccidium.

Before leaving the question of the comparison of feeding areas of well and badly burned moors, one further point should be mentioned. On a well-managed moor the heather fired is all under twenty years old, and when it is burned the young heather springs from the root the same year. On a badly burned moor, where old stick heather forms the main crop, the heather springs from seed,¹ and in many cases only affords food for Grouse after the area burned has passed through successive stages of grass and cross-leaved heather varying in point of time from six to twenty years. If the soil has a tendency to grow bracken the heather may be lost for ever. That is to say, in a fifty years' rotation moor, probably 20 per cent. of the moor is either black ground, bracken, grass, or cross-leaved heather, and is not yielding its proportionate quota of food. When we consider this loss of food area as well as the generally recognised fact that on a frequently burned moor the heather grows thicker and more luxuriantly than on one badly burned, it is no exaggeration to say that the food-bearing capacity of a moor at its best and worst is as ten to one.

This change in the flora of a moor after burning is specially noticeable in the case of accidental fires, such as occurred on a large scale in Yorkshire in 1887 and 1893. Accidental fires are commonest in very dry weather, and thus there is a danger of the peat and soil being burned to a depth of several feet, thus destroying the roots of the heather.

The second reason for burning is to keep the birds at all seasons split up over the ground. Grouse are not naturally gregarious, nevertheless they frequently get together into big packs for purposes of safety after frequent disturbance, or for shelter on the approach of storms, or in search of food, or to avoid snow or drought, or to prepare for migration, but, once the immediate cause of packing is removed, their instinct is to get away from their brethren and take up their family life apart. To help the birds to develop this instinct,

¹ Vide Pl. LVII. Fig. 2.

PLATE LVII.



FIG. 1. *Calluna vulgaris* (Common Heather or Ling).
Showing form of plant when growing from the root—first year's growth.



FIG. 2. *Calluna vulgaris* (Common Heather or Ling).
Showing form of plant when growing from seed.

the patch or strip method has been advocated in the past, and, provided always the strips and patches in their totality suffice to maintain the food yield of the moor at its highest, no better system could be adopted. Strips and patches.

The minor point of whether narrow strips or square patches are advisable is not worth discussing; keepers have their fancies, self-appointed authorities will air their views; it is probable that both methods can be used with effect, each to suit the special circumstances of individual moors.

The object to be aimed at is clear, that every bird should have its tufts to nest in at the edges of the burned ground, its bare ground to sun itself in and on to which to take out its chicks; its older Apportionment of heather. heather for concealment, its breast-high 10-inch heather for feed, its well-matured heather for seed and shelter in winter, and, finally and of most importance, its six- to fifteen-year-old heather to keep it in health and vigour in early spring.

In cases where it is impossible through the wetness of the season, shortness of labour supply, etc., to get the moor thoroughly burned in strips or patches, it may be asked whether it is not better to abandon the small patch system and burn a large acreage of moor? The answer can be given with no uncertain voice—patches are only a secondary consideration, the first essential is to get the proper proportion of the total acreage of the moor burned each year. Apart from the destruction of Strongyle larvæ by fire it must never be forgotten that it is the sufficiency of the food supply that enables birds to stand a heavier infection of this parasite. On Broomhead and Moy moors, which carry regularly the highest stock per acre and are among the best burned moors in England and Scotland respectively, the patches burned are large and disease is practically unknown; but so also is stick heather!

Having laid down the reasons with regard to food supply which make heather burning necessary, the next thing is to consider the various Methods of burning. qualities of soil and heather into which a moor is divided, discuss the treatment of each and look into the limitations, some natural and some artificial, which stand in the way of a complete realisation of the object in view.

Old heather should be burned in strips, for when old stick heather is burned the fire is so hot that the roots are charred and killed; in Old heather. this case regeneration can only proceed from seed, and if the burned areas are narrow, self-seeding is materially helped by wind-blown seed.

While it is necessary to burn off blocks of old heather in strips, it is advisable at the same time to get a considerable area burned on one beat of the moor.

Sheep always rush to the newly burned ground for the sweeter grasses that grow there, and unless there are good stretches of burned ground for them to feed on, they will concentrate on the small isolated patches Danger from sheep. and pull up all the young heather plants as they spring from seed. Every one who is acquainted with a moor in autumn must have observed the hundreds of little brown shrivelled-up heather seedlings pulled up by the sheep's teeth on every patch of newly burned ground.¹ To obviate this wholesale destruction it is sometimes considered advisable, where the sheep stock is heavy and the moor has a tendency to go back to grass, to fence off areas of old stick heather for two or three years after burning. This gives the young heather a chance of coming away, and once rooted it can defy the efforts of the stoutest-toothed "black-face."²

Old heather should, whenever it is possible, be burned "against the grain," that is to say, against the lie of the heather sticks. Burning "against the grain." "Back-firing" or burning against the wind gives a very clean burn, the fire travels slowly, and destroys not only a larger percentage of the stalks of the heather, but also burns into the "fog" or moss which surrounds the roots of old stick heather. Owing to the shortness of the time available for burning in an average year, dampness of the soil, etc., "back-firing" is not always possible. In the case where an overcrop of partly charred sticks have been left it is advisable to run a fire through the burned ground a second time if possible in the second or third year following the first burn. This Second burning. second firing has the effect of clearing the ground of the charred heather sticks and burning off the moss which, having been exposed to the air, is drier than at the first time of kindling. This affords a good clear seed-bed on which the wind-borne heather-seeds rapidly establish themselves.

The very greatest care must be taken of steep banks, especially those Steep faces. facing south, as these are the places that in time of snow give shelter and food to the Grouse. It must be understood that careful treatment does not mean allowing such places to run into old stick heather. Many keepers are so frightened of touching these winter feeding-places that on many moors the heather in these places has become rank, and is

¹ *Vide* Pl. LVII., Fig. 2.

² *Vide* chap. xxii. p. 501.

rapidly losing its value as winter food. Burning on steep banks should be carefully done so as never to reduce the total yield below the minimum which is necessary for food in time of snow.

In the interest of both sheep and Grouse wet "flow"¹ ground should be burned in big stretches outside the ordinary rotation—if possible once "Flow" in every six years. Flow ground usually overlies deep, damp peat, and ground. is therefore protected from the full effects of the fire; the grass and the stunted heather in consequence come away quickly from the root. It is often difficult to burn flow ground owing to the heather being broken up into tussocks, and the driest weather should be chosen for the task.

Knolls and hillocks are the favourite haunts of the Grouse, and however small they are, never more than one-third should be burned at one time; the keeper's aim should be to provide in this way both food and Knolls. cover for the birds frequenting them.

The keeper should invariably get at the northern slopes of his ground as soon as the opportunity occurs. On high moors late snows North slopes of hills. make this possible only once in half a dozen years.

Grey heather killed by snow or frost should be burned wherever it appears; it is absolutely useless for food, and serves no purpose beyond cumbering the ground. Probably also heather which has been damaged by beetle should always be burned, as it is very doubtful whether it ever recovers from the attack of this pest.

Peat hags should be burned when the ground is not too dry. Grouse are particularly fond of broken peat ground, and the food supply of short gnarled heather that grows there should be maintained at its highest. The Peat Hags. peat itself occasionally gets on fire, and has been known on occasion to burn right down to the bed rock. In one or two cases that have come to the Committee's notice excellent heather has grown on the mineral soil thus exposed. As the new growth in such cases may take twenty or thirty years to come up, such burning is probably outside the rotation that even the most progressive of moor-owners would care to adopt.

¹ By "flow" ground is meant the flat stretches of peaty land where, owing to the retentive nature of the soil, the surface water lies in pools and channels between tufts or tussocks of heather; it is to be distinguished from marshy or boggy land where the water lies in suspension below the surface. Flow ground cannot as a rule be drained owing to the absence of a natural "fall," and even when drains are cut the nature of the soil is not sufficiently porous to make them effective. Flow ground grows a poor quality of stunted heather usually mixed with sour-looking grass, yet Grouse are often found to frequent it during the daytime, especially when it lies on a high plateau or immediately under the crest of a ridge.

The sides of burns and streams are most important features on a moor; they are the favourite nesting places of Grouse, they afford shelter during storms, and are places where food can be obtained in times of snow. They should be carefully burned in very small patches, special care being taken to clear up the immediate burn-side and prevent its being used as a shelter for vermin, particularly for stoats, who otherwise use it as a convenient covered way to reach their prey.

It is hardly necessary to point out that in burning a moor the keeper must consider the method in which the shooting is carried out. In the case of the driving moor broad belts should be burned immediately in the rear and patches immediately in front of the butts to facilitate the "picking up" of Grouse; settling ground with good cover should be left in the direction towards which it is intended to drive the birds. In the case of "dogging" moors, favourite banks should have a special allowance of long heather into which the birds can be worked at the end of the day. In deer forests "the beds" on which deer lie on in the sheltered corries should be lightly burned.

Heather can be burned at all times of the year in England. In Scotland, by statute, heather-burning is confined to the period from November 1st to April 10th. On high wet moors an extension of the period to April 25th can be obtained. In Wales, by custom, burning is usually carried on during the spring months.

As soon as it was established that the health of the Grouse depended not only on the distribution of edible heather, but also on the total extent of the supply, it became a matter of primary interest to the Committee to decide whether in their opinion the burning season should be extended, and how the results of autumn- and spring-burning were to be compared.

The investigation was begun by sending an inquiry-paper to correspondents, asking for their experiences of autumn-burning; the time taken for heather to grow again when springing from the root and from seed respectively; the opinion of sheep farmers as to the merits of the two methods and the character of soil least and most suitable for autumn-burning, based on a comparison of results obtained. In neighbourhoods where heather had never been regularly burned in autumn, correspondents were asked to burn patches in spring and autumn side by side and to compare the results.

The idea was intelligently taken up and thoroughly worked out, from the south of Wales to the north of the Highlands.

The results of the observations taken have brought the Committee to the following conclusions:—

- (1) That in the interests of sheep and Grouse autumn-burning is advisable on all moors.
- (2) That it is necessary on large moors.
- (3) That it is the only possible method of getting high ground with a northern exposure into a proper rotation of heather crop.

The Committee are further of opinion:—

- (a) That in the North of England the evidence goes to show that, whether springing from the root or from the seed, the growth of heather following autumn- and spring-burning is identical.
- (b) That on the more northern moors the heather is probably slightly slower in reaching maturity after autumn-burning, especially on shallow peat or hard ground.
- (c) That, while there is a certain prejudice, especially amongst older keepers, against autumn-burning, this prejudice did not appear to be founded on substantial grounds; as far as the Committee were able to learn, the majority of those who expressed themselves opposed to autumn-burning were found on examination not to have themselves tried it, and to have based their opinion either on general reasons or second-hand information.
- (d) That on 95 per cent. of the moors in England on which autumn-burning had been tried the practice had been continued with the full sanction and approval of the sheep farmers interested.
- (e) That at least 75 per cent. of the larger moors examined are insufficiently burned, and that in many cases an extension of the burning period would enable a larger stock of both sheep and Grouse to be maintained.
- (f) That autumn-burning is necessary in the interests of the health of the Grouse and sheep, and that legislation in Scotland making it permissible to burn after October 1st should be introduced into Parliament without delay.

With a view to further ascertaining the opinions of sheep-farmers on the subject of heather-burning, a meeting was arranged between representatives of the Committee and a number of sheep-farmers from different districts. The views expressed clearly indicated that in the opinion of sheep-farmers there is not enough heather burned for either Grouse or sheep

Opinion of
sheep-
farmers.

on the majority of moors in England and Scotland, and that there is a general wish on the part of sheep-farmers on heather ground that more heather should be burned. The farmers further stated that they would be glad to try autumn-burning in co-operation with owners, and that they could probably give more assistance in the autumn than in the spring, because in the spring they are usually busy with sheep that have returned from wintering, and with the superintendence of their stock during the lambing season. They considered that it matters little whether autumn-burned heather grows as well as spring-burned heather, the great object being to get rid of the large tracts of old useless heather which are of no value either for Grouse or sheep. They confirmed the view of the Committee that high ground with a northern exposure can only be burned in the spring in very exceptional years.

The sheep-farmers further drew attention to the following points:—

- (1) That where heather is allowed to grow too old, there is a danger of its place being taken by bracken after burning, whereas if the heather is burned young the fresh growth has more vitality and usually defeats the bracken.
- (2) That old heather is undesirable because after burning many "burrens" or bare sticks are left which tear the wool off the sheep's bellies.
- (3) That sheep-farmers prefer the heather to be burned in large patches, because otherwise a large enough area is not burned each year; but that they have no objection to burning in small patches and strips, provided the total area burned reaches the full proportion proper to the moor. This proportion was estimated at from one-ninth to one-twelfth of the total acreage.

On the actual methods of carrying out the burning there is not much to be said. The gear is simple; a birch broom and a paraffin firing lamp.¹ The necessary party of six or eight men under a keeper can work in pairs on a calm day with a fairly dry moor, the keeper starting the fire, the couples guiding its course, extinguishing and controlling it as occasion demands. In windy weather, or when the heather gets dry, the whole party have to act together, and in consequence, though the individual burning may be done at a quicker rate, a smaller total area will be got through in a day. As a health-giving exercise heather-burning has much to commend it; it is particularly hard work and trying to clothes, temper, and especially to the eyes.

Methods of
procedure.

¹ Special lamps are sold for the purpose.

The Committee have now laid down the object of heather-burning, the methods of treatment of different types of ground and certain laws applicable to all moors; it only remains to discuss the practical steps the owner of a badly burned moor must take to get his heather-land into "good heart" with the least possible delay. We will presume for the moment that the moor under consideration is one of those many moors in England or Scotland which has possibilities, but which has been neglected; a moor which has its high ground difficult to burn, its boggy undrained land, and its stretches of stick heather with a tendency to revert to grass; that, moreover, it is a moor which has disease at irregular intervals as well as average and bumper years; and that, like all moors that form part of a tract of Grouse ground, it is liable to be overstocked at the critical period of late winter and early spring.

The first thing that the owner of a moor of this sort must do is to decide what rotation of heather crop is to be aimed at, i.e., what is the total area of moorland available, and how many acres of it are to be burned every year.

The period of rotation requires very careful consideration, and depends on the average age of the heather, the sporting results the moor-owner wishes to obtain during the period of transition from bad conditions to good, and the local difficulties—labour, climate, etc. From what has been stated on the results of burning stick heather, it is evident that if really old heather bulks largely in the total area it is impracticable to jump at once into a fifteen years' rotation and maintain any stock of Grouse. A little calculation will show that in the extreme case of a moor on which all the heather has reached the "keeper's delight" stage, and therefore requires six to twenty years to come again, to burn the whole moor in fifteen years would leave not only no spring feed, but scarcely any edible heather at all.

In treating a really badly burned moor, therefore, unless it is determined to sacrifice several years of sport and set all the old heather ablaze, less heroic methods should be adopted, and the ground be got gradually into a shortened period of rotation. To fix how long this intermediate period should be, it is necessary to go carefully over the burned ground of the last decade in order to see how long the general average of burned heather takes to come to maturity. This will vary, not only with the age of the heather, but with the elevation of the moor, the climate and exposure, the depth of peat, the amount of flow and hard ground, and the stock of sheep. By carefully noting the results and

comparing them with similar results on well-burned moors, it will be possible to arrive at sufficient data to give the number of years for the first rotation.

It is probably generally true to say that on a moor on which heather grows readily, and on which all the heather is burned before it has passed its best, heather springs from the root the year it is burned, and comes into flower sometimes in the first and generally in the second or third year. That on a badly burned moor situated 600 to 1,200 feet above sea-level the ground covered by partly withered heather of an average height of 2 feet will remain black for two years after burning, that for the next three to five years it will be covered by grass and cross-leaved heather, and that six further years will be necessary before there is a full yield of edible *Calluna* heather. This will mean a handicap of nine years, and on a moor of this sort a rotation of twenty to twenty-five years should, in the first case, be attempted. It must not be thought that for the whole of these nine years the ground is useless. During that period it is useful for old birds as a basking-ground, and for young chicks as a feeding-ground; and the early grasses and seeds and even ferns that grow there are not without value. It will afford, however, little or no spring food.

Having fixed the rotation and the acreage to be burned, the next thing is to decide on the allocation and size of the individual patches or strips. We will suppose that the badly burned moor is one of 4,000 acres, that there is a sufficient labour supply, and that the rotation attempted is to be one of twenty years (*i.e.*, one-twentieth of the heather ground burned per annum). The amount to be burned every year would be 200 acres; but to make up for bad burning seasons 300 acres should be attempted whenever seasonal conditions permit.

To burn this area in patches of one eighth or one fourth of an acre is obviously impracticable; even allowing for an area of 50 to 100 acres being burned in big blocks (flow ground or high ground with a northern exposure), it would be impossible to burn the remaining twelve hundred odd strips necessary to make up the total acreage prescribed. It is therefore necessary to decide on certain general lines of moor-burning which will give the necessary total area burned, and still maintain the patch system as far as possible. This will be obtained by treating each type of heather on its own merits.

Example of scheme. 1st. To burn old heather in strips 50 yards wide, and let the strip run as far as the fire will take it.

- 2nd. To burn average foot and a half heather in strips and patches of one fourth to one half of an acre.
- 3rd. To burn patches and strips on the steep faces of the wintering ground in small blocks of not more than one fourth to one tenth of an acre each.
- 4th. To burn the burn-sides, knolls and nesting grounds of Grouse, in even smaller plots.
- 5th. To burn the wet flow ground in big patches of 1 to 10 acres.
(*N.B.*—This should be done so as to cover the flow ground every six to nine years.)
- 6th. To burn the high ground with a northern exposure in large 3 acre blocks.
- 7th. To burn good broad strips round each of the boundaries.
- 8th. To treat specially those portions of the moor which have a tendency to revert to grass.

By adopting these methods with, say, three keepers (watchers to count as keepers), each in charge of two parties of two or three men each—a total of from fifteen to twenty-one burners—it may be possible to get the work done. The burners will have to fire twenty patches of 1 to 5 acres, say a total area of 50 acres, 300 patches of from one fourth of an acre to one acre, making, say, 150 acres, two hundred patches of from one fourth to one tenth of an acre, say 50 acres, *i.e.*, about 500 burns with a total of between 250 and 300 acres.

Taking the average as four parties burning a day, for it must be borne in mind that on very dry or windy days the keepers will often have to use the whole of their posse as one burning party, it will require about ten days or twenty half days to get through the work, calculating that each party burns an average of fourteen patches a day.

This is a fair statement of what ought to be done on a 4,000-acre moor; it probably exceeds by a very considerable amount what is done on many moors of double that size.

If the number of men for the burning parties cannot be got the area of the fires must be bigger; but the ratio of heather burned to total area of the moor must be maintained at all costs.

In considering the general question of heather burning, undue weight must not be attached to arguments such as the following:—

- (1) *That the expense is too great.*

Arguments
against ex-
tensive
burning.

Apart from the question of sport, this argument can be proved to be erroneous in mere pounds, shillings, and pence, for, as has been shown already, moors can be raised from a yield of under three hundred brace per annum to over three thousand, or, expressed in terms of existing values, from £300 a year to not less than £3,000. Even on moors where such great advances cannot be made, the avoidance of a single year of disease would alone save more than three times the expenditure incurred in a decade through the employment of a few extra men for burning.

- (2) *The argument that the old keeper frequently puts forward that "to strip the moor is sufficient."*

It is not necessary to deal with this point again; it is sufficient here to point out that keepers have not the least idea of what acreage they burn in a year, and will often say and believe that they burn one-tenth part of the moor when one-hundredth is nearer the mark.

- (3) *The argument that the existing method of burning has produced good results in the past.*

This must be accepted, but with the reservation that good results in the past have almost invariably been followed by disease in the following year. It is to avoid disease and heighten the average yield of the moor that the progressive landlord will see that it is worth while to limit the food crop for a few years in the attempt to get the moor into good "heart."

- (4) *The old-heather argument that it is dangerous to burn the old heather as birds will have no food in winter.*

Three things should be remembered in this connection.

- 1st. That on some of the most heavily stocked Grouse moors no old heather exists, yet there is enough winter food.
- 2nd. That in time of snow the medium-sized heather can be raked with little labour and thus afford abundant winter food should the bulk of the long heather be buried in snow or destroyed by frost.
- 3rd. That long heather is valuable only as long as it gives food—*Grouse eat heather shoots, not wood*. Much of the heather in England and Scotland that has been left for winter food has been steadily going back for twenty years, and it now produces barely one-tenth of its proper food yield.

- (5) In a good burning year keepers often wish to knock off "work" under the plea that enough burning has been done for a single season. It is very doubtful if too much burning can ever be done in any season *provided the areas of the fires are reduced in size as the patching and stripping of the moor progresses*. By large fires a moor can be easily burned out, but no old patch is so small that a smaller patch cannot be taken out of it and the moor be thereby improved.

Certain moors or portions of moors have a tendency to go back to grass, and therefore require special treatment. The most common reasons for this reversion from heather to grass is lack of attention during the period from 1850 to 1900, overstocking by sheep (especially of the black-faced variety), and big fires after the heather has got old. In practice it is found that these causes often work in combination.

Treatment
of green
ground.

The attention of gamekeepers should be directed to the burning of "white grass" as well as heather. By doing so they provide directly for the sheep and indirectly also for the Grouse; for, so long as they are plentifully supplied with grass, sheep will not draw heavily on the heather. "White grass" can be burned in larger stretches and consequently more rapidly than heather, and advantage should always be taken of any specially dry season to burn the low, damp hollows where this grass chiefly abounds; in four seasons out of five such places are too damp to burn.

To bring green ground back to heather is always a slow and often a costly business.

Control of the sheep stock to prevent an over-cropping of the heather seedlings, fencing of the newly-burned patches, sowing of heather seed in specially prepared ground are all methods that may be found useful.

The methods of procedure and the respective values of "green" ground for sheep and Grouse are discussed at some length on p. 499.

The *laissez faire* argument—that the change from heather to grass or bracken depends on the seasons, and that nothing should be done—is one that the Committee view with suspicion. Putting off burning where old heather exists only means putting off the evil day, and it is probably correct to say that for every year that the old heather is left unburned after maturity, at least one year is added to the time required for the young heather to replace the grass.

There can, unfortunately, be no doubt that bracken is spreading considerably

on very many moors in the south and west of Scotland, and that not much effort is being made to combat this pest. Thick bracken will rapidly destroy both grass and heather, but of the two it is probable that the heather will be the more easily destroyed, and if bracken has once taken possession of ground for a period of years it will be found, on clearing the ground by regular cutting, that grass will probably come where heather formerly flourished. It is a common experience, when burning fairly old heather, to find that the few bracken stems which existed among the heather give rise to a much thicker crop on the bare ground, and may entirely choke the fresh growth of young heather.

Despite most careful investigation by the Highland and Agricultural Society, and other interested bodies, no specific has yet been discovered to cure the bracken trouble.¹

In the course of their investigations the Committee have noticed that bracken very seldom grows on crofter "soumings" where there are many ponies. While they do not feel that they have enough evidence on the subject to claim that this is a solution, they mention the fact as one which may be worth further inquiry and experiment.

In considering the general question of heather-burning, blaeberry ground has been dealt with as heather ground, and its further treatment need not be gone into in any detail. It is unfortunate that sheep are specially fond of the blaeberry plant in its younger stages, and on moors carrying a heavy stock of sheep this valuable plant is often grazed down to the root. Grouse eat blaeberries (buds, leaves, and berries) with avidity; even the caterpillars that infest the plant in early summer are a source of food-supply for young birds. It may be noted from an examination of the tables of crop-contents that the consumption of blaeberry by the Grouse is irregular, and the percentage seems to depend more on the general supply of food than on any tendency of the birds to eat the plant more in one month than another.

From statistics collected, blaeberries appear to form 30 per cent. of all the foods taken by the Grouse in Derbyshire; 22 per cent. in Yorkshire; and 11 per cent. in some of the counties of Scotland. Undoubtedly a good deal could be done to increase the food-yield of the moor by encouraging the growth of this hardy plant, either by fencing off areas where it is eaten down by sheep or by planting it in suitable places.

Colonel G. J. Fergusson-Buchanan of Auchentorbi has recently printed a pamphlet setting forth the success which has attended his efforts to get rid of bracken on heather and grass land.

DRAINING.

Close observers of "Grouse Disease" have always held the idea that the mortality has been in some way connected with the wet, undrained portions of the moor. Scientific investigation shows that there is probably a good deal of truth in this view. The Strongylæ larvæ have been shown to pass the free-living portions of their lives in damp surroundings. Even in frozen water they appear to live for an indefinite period, whereas complete drought may kill them in a very short time.

Without putting drainage forward as an absolute specific against disease, it can be urged with confidence that a well-drained moor is less liable to dangerous infection of nematode worms than a moor with stagnant pools and great stretches of flow ground. Draining should be done with care and on a well-considered plan. Nothing is more common than to see the water carefully drained from the top of a hill-face descending only to flood a much larger acreage below, owing to there being insufficient drainage arrangements for carrying off the surface water thus collected.

It will generally be found advisable to employ a professional sheep-drainer, and allow him to work by contract at a fixed price per chain. The specifications must ensure that the drain is clear cut, at least the breadth of a spade at the bottom, that the sides are at a slope of not more than one in two, and that the turf dug out is thrown away not less than 6 feet from the drain. Shallow drains made in this way reduce the danger to the young Grouse, and are also less liable to choke and flood the moor. Drains should be made on the herring-bone pattern, and begin with wide arms high up the hill-face to catch the surface water. Special care must be taken that the central drains are sufficiently large to allow the water collected to run off easily into a main burn. The ground that it is desirable to drain is not the flat sodden bog or sour flow land, but the ground on which the fog or moss has only recently begun to choke the heather.

Draining, when undertaken, should be thorough. It is better to confine the area of work and watch results, with an occasional clearing of the drains, than to spread the work over a great extent of country where little immediate result is seen, no attention is paid to upkeep, and the lie of the drains is soon lost. On most moors money would be well expended in draining, for not only would the risk of infection be thereby lessened but the total yield of heather would be increased. The supply of grit which drain-making is apt to expose is not a trifling consideration to the general health of a moor, as will be seen in chapter v.

CHAPTER XIX

THE HEATHER BEETLE

By Percy H. Grimshaw

Part I.—On “Frosted” Heather and its Connection with the Heather Beetle, Lochmæa suturalis.

FOR a long time the attention of many proprietors of Grouse moors and their keepers has been directed to the fact that large patches of heather, varying in size from a few yards square to hundreds, or even thousands, of acres, have turned a rusty red or withered grey colour, and have become useless as food for Grouse. In the districts which suffered most from this condition large numbers of the Grouse have left the affected area and migrated to neighbouring moors where the heather was in a healthy state.

Not only does the shooting value of such a moor become thus seriously impaired, but the health of the birds themselves is affected. Although there does not as yet appear to be any direct connection between the diseased state of the heather and “Grouse Disease,” inasmuch as the birds have been proved not to eat the withered shoots, yet the deficiency of food on an affected moor undoubtedly results in a weak state of health, rendering the Grouse less fit to resist the attacks of tapeworms and other parasites, or to combat disease of any kind whatsoever.

It is, therefore, of the utmost importance to ascertain, if possible, the exact cause of this blighted condition of the heather, and to devise some practical remedy.

During the progress of this Inquiry many letters have been received by the Committee which serve to show the great extent of heather affected in various parts of the country. Diseased heather has been reported from moors in the counties of Nairn, Perth, Inverness, Argyll, Ayr, Lanark, Kirkcudbright, Dumfries, Selkirk, Roxburgh, Fife, Cumberland, Yorkshire, and Montgomery.

From this list it will be noted that the blight has been met with principally in the western districts; but this may be due to lack of information from the east, and it is hardly advisable at present to lay much stress upon the distribution of "frosted" heather as indicated by this correspondence alone.

The following extracts from the correspondence may be interesting as indicating what has hitherto been observed with regard to the extent and nature of the ground affected, the time of year when it is chiefly noticeable, and other points. The names of localities, and those of the proprietors and keepers have, for obvious reasons, been suppressed; but at the same time the Committee would here express their indebtedness to all who have thus contributed information.

(a) "Diseased heather 'an acre in extent.'"

(b) "First noticed about the end of August last. . . . As there was no frost at the time, it struck the keeper and myself as somewhat curious."

(c) "(1) The rusty red is from ground which has become affected since last October; (2) The dark grey piece is from ground which was attacked two years ago."

(d) "There are great areas, and many patches, of this brown, withered heather on the moor."

(e) "I am sending two samples of heather for your inspection. I am sending one of young heather, which has turned quite white and withered looking, and is growing on the side of a hill facing the south-east. The other sample is off a large stretch of level, wet, mossy land. It seems to grow till a certain height, and then to die away."

(f) "There are several patches of considerable extent over the whole moor, which look similar to the part off which I took the heather I sent you for examination. Should the disease spread to any great extent, it might become damaging to the feed of the Grouse. . . . I have seen no heather affected which is under five years old; all parts affected are from six years upwards."

(g) "There is far more rotten heather on the low moors at this season than there was when I wrote to Mr —, and on an adjoining property it was very bad this season, while it was almost unknown a couple of seasons ago. In my opinion this spoilt heather will prove a very serious question in the near future for the proprietors and tenants of Grouse moors."

(h) "My keeper says it [*i.e.*, diseased heather] was confined to the young heather, and the old was not frosted at all. Also the west end of the moor,

about 2,000 acres, was bad with it; and there was none on the remainder of the moor."

(i) "I have forwarded to your address a sample of heather that showed signs of being frosted in July last year. It turned a rusty red, and some of it grey between July 8th and 24th. It was on the latter date that I noticed it—there would be nearly 2 acres in the patch affected."

(j) "The damage done on my own estate was not very serious, but in neighbouring places it was much worse. . . . With regard to the permanency of the damage, I do not think there is much fear. I examined some of the ground as recently as yesterday, and find that even where it has the withered grey look, the twigs are green under the bark; only in a few cases is the previous season's growth dead, and in no case is the two-year-old growth destroyed. . . . I should have stated above that the damage has only occurred where the ground was very cold, wet, and waterlogged—the sort of ground on which, even when drained, it is useless to plant forest trees."

(k) "We think the damage is chiefly, if not entirely, confined to places where the sun strikes during the day, and especially in the morning. . . . My ground faces chiefly north-west and west."

(l) "With regard to your inquiries on the subject of rusty red heather, we have noticed several small patches of this all over the moor, and the majority of them are to be seen on the south-west and south faces of the hill, and a fair amount was to be seen on the low ground at . . . This burned appearance first showed itself during the hot weather in the month of July, and that is the time that it is noticed each year according to keepers and shepherds. It is, of course, useless for Grouse-feeding purposes."

Now this peculiar and serious condition of heather was, up to a comparatively recent period, universally attributed to the action of frost, whence the popular name of "frosted heather," and even at the present time this opinion is firmly maintained in some quarters. After a careful investigation of the subject the Committee are now in a position to assert with some degree of confidence that the damage is the work of an insect. My own attention was first drawn to the question in the month of August 1897, when I received from a correspondent in Ayrshire a patch of heather, the shoots of which were brown and withered, while among the roots were a number of small grubs and pupæ. My correspondent thought that the damage was caused by these insects, and at the same time he suggested that the diseased condition of heather which

was so widely known as "frosted" was identical with that of his specimens, and due to the attack of the same species of insect. Acting upon this suggestion, I examined the soil about the roots of this sample, and also of two others sent by the same gentleman a few days afterwards, and found therein numerous examples of the insect in all stages between that of fully-grown larva and mature insect. I succeeded in identifying the creature as a phytophagous beetle known as *Lochmæa suturalis*, Thomson, and immediately published a short account of it, with figures, in the "Annals of Scottish Natural History" for January 1898 (pp. 27-29).

I thought little more of the matter until it was again brought to my notice in connection with the investigations of the present Committee. In order to obtain more evidence, either for or against the theory that the beetle was alone responsible for the damage, a circular was issued in January 1909 asking for reports from correspondents regarding the extent to which their moors had suffered from diseased heather, and requesting samples to be sent to me for examination. Before and after the issue of this circular I received typical examples of "frosted" heather from many sources, and it is important to note that *in every case where the shoots had changed colour* the leaves were undoubtedly nibbled by some insect, this being easily shown by examination with a hand lens. Not only were the bases and edges of the leaves eaten, but in many cases all the leaf had disappeared except the mid-rib, which remained as a kind of bristle on the shoot. The specimens now in the possession of the Committee furnish absolute proof that in all cases of diseased heather submitted to them the rusty red withered appearance is associated with, if not entirely due to, the attack of some insect, presumably the beetle referred to above, and which we now call the heather beetle.

In order to ascertain if the beetle was actually present in the samples of heather sent—not by any means an easy matter—I devised a plan by which the little creature could be made to show itself. As all the samples were sent to me between the months of October and February it appeared to me probable that the insects, if present at all, would be in the mature stage, judging from what I had seen in the specimens examined in 1897. In all likelihood, too, they would be in a hibernating condition somewhere about the roots or surface of the soil. As it was impossible to find them without tearing to fine pieces every cubic inch of soil—a most laborious task—I hit upon the plan of soaking each block of soil, with heather attached, for several hours in water, gradually

increasing the depth of the water until the actual shoots of the heather were submerged. It was very interesting, one might even say exciting, to see the result. In every case a beetle appeared a few minutes after the sod had been placed in water, to be followed every few seconds by another, and so on till they had all been driven out. In this way I examined sixteen samples of diseased heather, and only two of them failed to yield specimens of the beetle; these failures must, I think, be attributed to the small size of the samples, for they were almost the smallest which I had received, measuring only $12\frac{1}{2}$ and 30 square inches respectively.

The following table indicate the numbers of beetles obtained from the samples by the above method.

No. of Sample.	Date.	County.	Size in sq. inches.	No. of Beetles obtained.	Remarks.
1	Oct. 13, 1908	Lanark	288	47	
2	Oct. 22, 1908	Argyll	288	70	
3	Jan. 26, 1909	Selkirk	144	18	
4	Jan. 30, 1909	Argyll	144	23	
5	Feb. 4, 1909	Ayr	60	52	
6	Feb. 5, 1909	Argyll	90	48	
7	Feb. 5, 1909	Ayr	64	36	
8	Feb. 6, 1909	Argyll	152	3	
9	Feb. 6, 1909	Cumberland	16	2	Very little soil sent.
10	Feb. 14, 1909	Argyll	$112\frac{1}{2}$	21	Badly diseased.
11	Feb. 14, 1909	Argyll	72	7	A few twigs diseased.
12	Feb. 14, 1909	Argyll	148	11	Very little diseased.
13	Feb. 15, 1909	Argyll	35	8	
14	Feb. 22, 1909	Argyll	$12\frac{1}{2}$	0	Very small sample.
15	Feb. 22, 1909	Argyll	30	0	Very small sample.
16	Feb. 22, 1909	Argyll	72	52	Badly diseased.

If these figures are worked out they show an average of 1,437,480, or nearly a million and a half beetles per acre. Thus *Lochmæa suturalis*, if the cause of the diseased condition, is an important pest, and cannot be ignored.

It may be of interest to give further extracts from correspondence, to show that the greater part of the evidence either actually supports, or at least is not in conflict with the idea that the heather beetle and not frost is the responsible agent in the devastation of so many acres of heather.

(aa) "The enclosed . . . larvæ I found yesterday on the ground amongst the grass and moss, where the heather is all dead and diseased. I thought

it might be the larva of the heather beetle, so thought I would forward them to you for examination." [Contents of box were nine larvæ and twelve pupæ of *Lochmæa*.]

(bb) "Here we had very little signs of the insect last year, but this year it is over-running the moor and doing great damage. The insect made its appearance in beetle form in May, and its grubs about three weeks or a month ago, and is now to be found in hundreds on every bit of 'rusty' and 'so-called frosted' heather. The grub appears to appreciate [? prefer] young to old heather."

(cc) "From what I saw . . . about six weeks ago, I have no doubt you are correct as to 'frosted' heather. There are great areas and many patches of this brown, withered heather on the moor, and there was a whole colony of the larvæ at the roots of every such patch we looked at."

(dd) "My keeper has had two days on the moor, searching for the larvæ or pupæ of the heather beetle, and he can find none. . . . I am sorry the search was not successful; but the information that the larvæ disappears between September 5th and November 5th amounts to something."

(ee) "On the . . . moors there were, in places, many patches of the so-called frosted heather—heather which had grown well up to a certain point, perhaps four to six years, and then without apparent rhyme or reason lost its sap and turned brown and withered before the flowering season. It looked very much like what heather might be expected to appear after a severe and late frost in May, but it was quite evident that atmospheric conditions (wind or temperature) had nothing to do with the result, as the 'frosted' patch ended quite suddenly and was abruptly framed in perfectly sound healthy heather, which must have been exposed to exactly the same external conditions as the 'frosted' heather. The keeper and I had many discussions over the cause of the spoilt heather, and we only agreed on one point, namely, that frost had nothing to do with the disease. I suggested a vegetable parasite, and he had views on improper burning, and there we left the matter (both of us being wide of the mark as it turned out). On . . . at the time I am speaking of, there was a very considerable quantity of the 'frosted' heather; I couldn't, even very roughly, give the acreage, but over the whole ground it must have mounted up to a big total, probably not much less than 750-1,000 acres. The 'frosted' heather is entirely useless for food, neither cattle nor sheep nor game will touch it so far as I know; therefore in this particular year the wretched and insignificant little beetle destroyed the agricultural and sporting value of (?) 1,000 acres on one moderate-

sized estate alone. How far the pest is spread over the whole of Scotland I don't know, but the total acreage of spoilt heather must be something very big indeed, and both the farmer and the game preserver have a very troublesome enemy to cope with in *Lochmæa suturalis*."

(ff) "It may interest you to know what we have been doing about the heather beetle—practically, they have damaged the whole moor, and we notice what I think was mentioned in your pamphlet, that they steadily work *eastwards*. We have been burning the affected heather as much as possible. At the time we were burning there was a very hard frost, and as regards the ground we turned up to examine we found the beetles not deep down as we expected, but clustered just round the root of the heather practically on the surface, and they didn't seem to be at all affected by the frost. I think it is a very serious thing for the moors in these parts, and hope that some effectual remedy may be found for them."

(gg) "I am sorry to say the heather beetle is very bad with us this year. It was seen on the wing first on April 5th in very large quantities. Now [August] the grub can be seen in the roots of the heather. The heather which was badly affected last year seems to be quite dead, and has turned white. We found in burning this spring that where the heather was burned in narrow strips the portions of heather left between were specially badly attacked, which looked as if the fire had not killed the grub, but had driven them to the heather close by. In cases where we burned one side of a knoll, we find the side left has not suffered. This may be simply a coincidence, but would appear to prove that the grub can move short distances to find fresh heather to attack, but cannot move more than a few yards. With regard to stock of Grouse, we have never had such a poor show, although some of the moors in this district have a fair average stock. I think we shall have to face burning a very large amount of the dead heather next spring."

(hh) "All the gamekeepers in this district obstinately maintain that the mischief is due to frost, but none of them can account for the fact of its only appearing in patches, and not by any means in the most exposed places."

(ii) "In the diseased heather I cannot myself locate either beetle or grub, although I've seen both many a time."

(jj) "I send you a portion of damaged heather with peat. . . . My keepers here scout at the idea of beetles, and say the damage came too quickly and over too great a radius, and they consider it caused by sudden thaw on frosted heather and bleak east winds following."

(kk) "There was a good deal of frosted heather all over this country, and I have referred to it in my Report sent in to Mr A. S. Leslie. In my opinion the heather beetle was not responsible for the damage, at least on my own estate. The burned patches of heather were plainly noticeable within two days of the severe frost which occurred on April 23rd, 24th, and 25th last. The heather was uninjured on dry slopes, most of the damage occurring in wet, cold and waterlogged ground, and the patches have not extended since they were first seen. On a neighbouring estate I understand that the patches have been gradually extending; but I have not verified this. I could understand the frost affecting places where the heather had already been damaged by the beetle; but one would expect the injured portions to increase afterwards, and the heather to be affected on dry as well as on wet ground."

(ll) Same correspondent as (kk). "It is very difficult for me to believe that the injury to the heather is due to the beetle, though I can well believe the beetle is a contributory cause. It is easy to find any number of beetles about the roots of the injured heather. The injured heather was all apparent immediately after the frost, and has not increased during the summer. It is also in places facing the morning sun as far as we can judge. . . . In looking at the heather all over the hill there seems no place where it is quite perfect, that is to say, there always seem a few injured or dead shoots when one looks closely at it."

(mm) "You will be interested to hear there is very little to be seen of the heather beetle this year, and this bears out our local experience of the pest, that after a wet winter the numbers and damage by them is very considerably checked, and that after dry winters they get bad again. This year we have had a very wet January and February, while these months in 1908 and 1909 were comparatively dry."

(nn) "In the *Field* for January 31st, 1903 (p. 150), Mr William Prior, gamekeeper to Lord H. Bentinck, Deeside, Dent (Yorkshire), writes as follows: 'It is a fallacy to suppose that frost injures the tender shoots of the young heather in the young Grouse season, or that the frosts of April, May, or June are injurious to the shoots.'"

(oo) "I don't think very much heather has been destroyed by grub, certainly some has, but a good deal of heather has been apparently injured by the severe frost we had some days ago."

(pp) "There were any amount of what I take to be the heather beetle

under the frosted plants; and if they are, there is no doubt of the cause of the blight. I am afraid it is only a severe winter which will do us any good."

(*qq*) "Regarding the ravages of the heather beetle, there is no appearance of it in this district at present. Several years ago I saw a large patch of heather affected as described in your circular, but burned the whole of it at once. I knew it was the work of some insect, but I saw no more of it."

(*rr*) "We are still finding heather destroyed by grub, but only in small patches. . . . It is in the spring, I think, when the harm is done, and we arrange to have most of the diseased part burned as early as possible."

(*ss*) "Am not aware of much damage to heather here, nor have I ever noticed any, except in the times when snow lay in sheltered parts for a fortnight or over; after the snow had gone the heather came back to its former colour. In this locality I do not think the beetle does any damage."

(*tt*) "I see we have several patches showing heather beetle; we have a moss about 1,000 acres and only 15 feet above sea-level; this moss is at least one mile away from high tide mark, so the damage is not due to the effects of sea spray. I see no signs of it on the higher ground."

On referring to the extracts here given (marked *a* to *tt*) the reader will gather that the damage is usually noticed between the months of April and August. As will be seen later, when the life history of the beetle is dealt with, these months are exactly those in which the beetle may be presumed to be in the egg and larval stages; fully fed larvæ are to be obtained in September, while the mature beetle hibernates during the winter, and has been noted on the wing in April and May (*see* extracts *bb* and *gg*). They would presumably pair and lay eggs in one or other of these two spring months, the egg state would only occupy a few days at most, and the larva would feed during the whole of the summer months. In most cases where the diseased heather has been examined *in situ* the beetles or their larvæ (according to the time of year) have been noted as numerous, and these observations form an interesting supplement to the figures actually obtained by experiment.

The districts from which damage from heather beetle is most commonly reported are those situated on the west coast of Scotland lying to the south of Oban. In Argyll, Ayr, Lanark, and Cumberland the pest is well known, whereas on the extensive moors in the northern and central Highlands of Scotland it is practically never heard of. It would appear therefore that the insect flourishes

best in a mild climate with a high average rainfall; but it is curious to note that after a very wet winter the beetles are not so numerous as after a dry one.

With regard to the position of the ground affected there does not appear to be any rule, for the extracts show the damage to be done on slopes which face all points of the compass from north-west through west to south-east. Again, the age of the heather liable to attack appears to vary, for while two correspondents report that *young* heather is chiefly affected (*h* and *bb*), other two note the damage as done to the plants of from four to six years old and upwards (*f* and *ee*). Most of the damaged heather occurs in patches, although these may extend over a large area, and there is a certain amount of evidence that low-lying wet, mossy ground is most subject to attack. This may indeed well be the case, for the beetle requires a good deal of moisture during the period of its metamorphosis from larva to mature insect, and during the course of my breeding experiments any pupæ which were allowed to become dry failed to develop properly.

Taking, then, the whole of the evidence into consideration, I am strongly of opinion that the condition known as "frosted" heather is entirely due to the attack of the heather beetle. Indeed, during the course of my experiments a patch of heather kept during the winter of 1908-1909 in a breeding cage in a warm room was eaten by a number of mature beetles kept in confinement. The condition of the shoots, after being nibbled, was undistinguishable in appearance from some of the samples sent in by correspondents for examination, and in this case frost was, of course, entirely out of the question. This experience is additionally interesting as proving that the mature beetle, as well as the grub, feeds upon the leaves.

The question of remedy alone remains for consideration; but this is a matter which presents some difficulty. It is obviously impossible to use any of the ordinary insecticides, as almost any chemical substance sufficiently poisonous to kill the grub or beetle would be very deleterious or even dangerous to the Grouse, to say nothing of sheep. The great extent of the area to be dealt with in most cases of attack is also a serious deterrent to the use of spraying mixtures.

Extensive draining of damp, mossy flats might be indirectly beneficial as a preventative of beetles, and would be directly beneficial to the moor in other respects. But draining is an expensive business, and except in districts where the ground can carry a heavy stock of Grouse, or is valuable for pasture, it may be better policy to allow the low-lying flats to remain in a water-logged condition.

Another remedy that suggests itself as, at any rate worth trying, is the

introduction of some creature which would feed upon the beetle or its grub, and so keep its numbers well in check. Unfortunately the Red Grouse itself does not appear to devour the insect at all, but a close relative, namely, the Black Grouse (*Tetrao tetrix*) has been proved to have what may prove to be a fortunate partiality for *Lochmæa suturalis*. I have strong evidence, from two independent sources, of the truth of this. In December, 1908, Mr Eagle Clarke, Keeper of the Natural History Department, in the Royal Scottish Museum, received a small box filled with beetles, from Mr James Sword, of the Smith Institute, Stirling. In the accompanying letter it was stated that the beetles formed part of the contents of the crop of a Blackcock and had been sent to Mr Sword for identification. The rest of the contents consisted of the seeds of *luzula* and sheeps *bitscabious*, and nothing else so far as could be seen. The beetles, of which there were a great many, were handed to me, and I at once recognised them as our old friend, or rather enemy, *Lochmæa suturalis*. Again, in 1907, Professor E. B. Poulton, of Oxford, communicated to the Entomological Society of London an interesting account of the food of Blackgame, based upon observations made by Dr F. Menteith Ogilvie, of Oxford, to whom I here express my indebtedness for the reference. In this communication Dr Ogilvie's notes on the contents of the crops of five Blackgame are reproduced, and in four cases out of five the heather beetle had been consumed in large quantities. These notes are of so much interest in the present connection that I cannot forbear quoting those portions which refer to the beetle. The summarised contents of the crops, numbered 1, 2, 4, and 5, include the following :—

(1) "An immense number of small dark brown beetles, *Lochmæa* (*Adimonia*) *suturalis* of Thomson."

(2) "Many dark brown beetles, as in ♀ of October 17th, 1907 [No. 1], but less numerous."

(4) "Three hundred or more dark brown beetles (*Lochmæa suturalis*)."

(5) "Immense number of the usual small dark brown beetle."

"The two outstanding features are the spangle galls and the small beetle. Almost all the birds were crowded with these, and, judging by my specimens, the Blackgame must have been destroying enormous numbers of both. I don't think, as regards the beetles, it is any exaggeration to allow three hundred beetles per day per bird. Ours is not a very good Blackgame ground now, and perhaps we have three hundred head in all; that would equal ninety thousand beetles

per day. I was surprised to find, too, how little heather was eaten in most cases, despite the fact that the birds were in almost every case found on the moor and not in the woods."

It is interesting to note that this was written and printed before any one realised the importance of the heather beetle as a destructive insect! I have been informed that on certain moors it is difficult to induce Blackgame to settle and make a home; but if they were once successfully established I cannot but think that they would become a useful means of preventing that wholesale destruction of heather which so often at present troubles the proprietors and keepers of our Grouse moors.

Probably the only practicable method of dealing with the pest is that of burning the affected heather, not at the usual season for so doing, but at the time when the grub is on the shoots feeding. As the beetle hibernates between the months of September or October, and April or May, it appears to me to be of little use burning within this period, for the beetles would then be lying in a torpid condition below the surface of the soil, with cool and moist surroundings, and the flames would pass over them without doing them serious harm. The burning should, therefore, be done between May and August, when the grubs are up feeding on the shoots. There are two principal objections to this plan, namely, the legal aspect of the matter and the practical difficulty of getting the heather to burn when in a green and sappy condition. As the present state of the law prohibits burning in Scotland between April 11th and November 1st special dispensation might be obtained in order to try the effect of burning the diseased areas during the summer months. The difficulty regarding the green condition of the heather might be got over by spraying the portion to be burned with some inflammable fluid such as paraffin or petrol, in small areas at a time, and well before any light is applied. This would have to be done with great care. It would not be necessary for the heather itself to be so thoroughly burned as in the ordinary operation for the purpose of promoting young growth for feeding, and I believe that the fire obtained from the inflammable agent itself might be sufficient to kill the grubs, even if the shoots did not burn so freely as at other seasons.

Part II.—The Life History of the Heather Beetle (Lochmæa suturalis).

The heather beetle (*Lochmæa suturalis*), whose ravages form the subject of Part I., is a small creature a little less than a quarter of an inch ($5\frac{1}{2}$ mm.) in length, of an oval shape, and usually of an olive-brown colour. It belongs to the family Chrysomelidæ, and was first described as a distinct species in the year 1866, by the Swedish entomologist, C. G. Thomson, in his great work on the beetles of Scandinavia.¹ It is very closely allied to *Lochmæa caprea*, Linnæus, a species which, as its name implies, feeds on sallow (*Salix caprea*). From this it differs in having the forehead more shining, the little black tubercles immediately behind the bases of the feelers more distinct and polished, while the whole of the thorax is more shining. Since both species have been thoroughly described in the various works, British and Continental, which deal with Coleoptera, it is quite unnecessary to do more than refer the reader to the figure given on Pl. LVIII. It is interesting to note that Thomson, in his original description, says the beetle is "not rare on *Salix repens* and other species of willow," while Julius Weise, in his account of the Chrysomelidæ in the "Naturgeschichte der Insecten Deutschlands," says it occurs "on marsh plants, also on birches and willows in marshes." Canon Fowler, on the other hand, in his "Coleoptera of the British Islands," states correctly that it is found "on heather, by no means uncommon, and very widely distributed"; but also adds: "it also occurs on birches and willows."

My knowledge of the life history of this beetle is yet, I regret to say, incomplete. I have never seen or received larvæ earlier in the season than the end of August, and by this date they are practically full-grown. From this stage, however, I have succeeded in rearing several specimens of the mature beetle, and have carefully noted the changes which take place, and the length of time taken to effect them.

The full-grown larva is represented in Figs. 2 and 3 of Pl. LVIII. It measures, when straightened out, about a quarter of an inch (6 mm.) in length, but it is usually more or less curved, and if disturbed rolls itself up close. It is of a dirty white colour, studded all over with dark markings and tubercles, which have a definite arrangement on each segment. The segments themselves are transversely wrinkled, while each tubercle is tipped with a fine

¹ "Skandinaviens Coleoptera," vol. viii. p. 151.

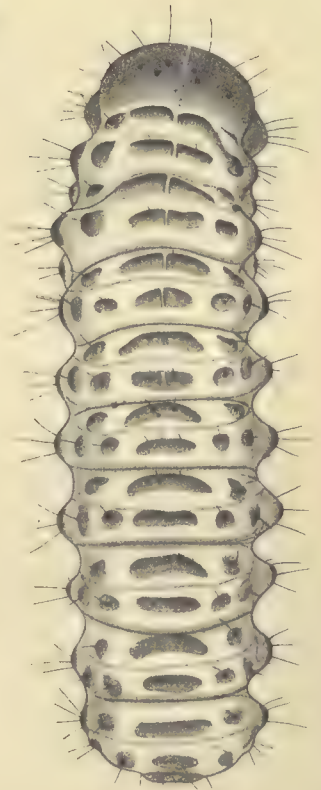
PLATE LVIII.



1.



2.



3.



4.

E. Wilson, Cambridge

bristle of a pale brown colour. The dark markings are arranged as follows:—Almost the whole upper surface of the segment immediately behind the head (that bearing the first pair of legs) is covered by a dark patch, which extends down each side to a level with the spiracles or breathing openings, and is divided down the middle by a fine line of the pale ground colour. Between this patch and the legs on either side is a small oblong dark patch two or three times as long as broad. On each of the two succeeding segments are two linear transverse dark marks, one anterior and the other posterior, and each divided in the middle like the patch on the first thoracic segment. On each side, opposite the extremities of each of these linear dorsal markings, is a more or less circular, but small, patch, the anterior one in each segment being smaller than the posterior; below these, on each side, is a large dark patch of a kidney shape with the concave side uppermost, and below this again two small marks on each segment. On the dorsal surface of each of the succeeding segments are two transverse linear markings, one longer at the anterior edge and the other shorter and placed at the posterior edge. Between these and the spiracles are three dark spots on each segment, one of which is anterior and in line with the longer of the linear markings, and the other two posterior and opposite the shorter. Below the spiracles a series of large more or less circular spots runs along the side of the body. The head is black and shining, and hemispherical in profile; the legs black, with the basal joints marked with white.

When the larva is about to pupate it crawls down to the ground and lies amongst the moss and stems of the heather, at the same time curling itself up into a sort of horse-shoe shape. The anterior half of the body becomes gradually stouter, and the larva adopts the peculiar and interesting habit of suddenly straightening itself and then reassuming the horse-shoe form. In course of time, by this means, the skin of the dorsal surface of the three segments behind the head splits, and the emergence of the pupa is gradually effected by wriggling. This process, as I have observed it, in favourable circumstances may be accomplished in twenty minutes, but may also take an hour or even more.

The pupa, when newly emerged, is of a creamy white colour throughout, with the exception of the tiny bristles about to be mentioned, which are blackish. The characteristic form of a Chrysomelid beetle is now distinctly traceable, while the legs, wing-cases, antennæ, and even mouth-parts can be recognised. Seen from above, the hemispherical thorax (prothorax of the mature beetle) occupies the most anterior portion of the body, and carries about a dozen tiny bristles,

four of which form a curved row near the posterior margin, and the rest a row near the anterior margin. In a dorsal view the head is quite invisible. The meso- and meta-thoracic segments, and those of the abdomen, are each provided with a row of four bristles, which are about equidistant from each other. Laterally, below the level of the spiracles, the abdominal segments are each tipped with a tiny bristle. Seen from beneath (*see* Pl. LVIII., Fig. 4) the pupa shows distinctly the legs folded up close under the body, and the antennæ beautifully curled under the two anterior pairs of legs and brought out again so as to show the tip of each close to the four anterior tarsi. Most of the joints of the legs may be distinctly seen, the posterior pair being folded beneath the wing-cases, which are bent round from the dorsal surface of the pupa and do not nearly reach the end of its body.

The first change to be noticed in the pupa is that on the fifth day after emergence the eyes begin to change colour, assuming a pale brown tint, while a couple of days later they are of a more distinct brown, and the separate facets may be distinguished. On this day also (the seventh) the extreme tips of the mandibles become darkened. Six days later the eyes have become very dark brown, almost black, while the mandibles are of a rich brown tint. When two more days have elapsed, *i.e.*, on the fifteenth day of pupal life, the tips of the mandibles are quite black, while the maxillæ have commenced to darken at the tip. On the seventeenth day the wing-cases, legs, and antennæ darken in colour, and the markings on the forehead, etc., characteristic of the mature beetle, are plainly seen, while on the eighteenth day the changes are fully accomplished, and the beetle emerges to enjoy a free and active existence. The pupal stage thus lasts, in a typical case, about three weeks.

The emergence of the beetle from the pupal skin commences with the liberation of the legs from the body, and occupies, judging from an example which I carefully watched, about four hours; but the elytra (wing-cases) are even at the end of that time quite pale, and only darken and harden quite gradually, assuming their permanent condition several hours later. The anterior legs and the antennæ are the first appendages to become capable of free movement, while the whole of the six legs are practically free in the space of an hour. As the struggling movements proceed, it is easy to notice the extreme thinness of the enclosing pupal membrane. It is apparently of considerable toughness, but is ultimately ruptured by the vigorous, movements of the limbs.

After observing the above details in the transformation of several examples, I placed all the newly emerged beetles, together with a large number of others received from correspondents, in a breeding-cage on a sod of healthy heather. In a very short time they had all disappeared, and in order to satisfy myself as to their whereabouts I detached a small piece of the sod (about 4 inches square), and tore it carefully bit by bit into small fragments. In this way I found in this small piece five beetles lying in a torpid condition in little hollows immediately below the surface of the soil. When the moss, etc., was gently torn off, the beetles were betrayed by their shining elytra, as they lay back *upwards*. They began to move when disturbed, and three of them got away and were recaptured. This observation tends to prove that the beetles assume the hibernating condition immediately after completing their development, which in most cases is effected by the third or fourth week of October. This date, of course, may vary slightly according to local conditions.

It is a matter for regret that I have not been able to trace the life history any further. Considerably over two hundred specimens were kept alive in my cages throughout the winter, and early in the spring of 1909 (March 2nd and succeeding days), under the influence of the sunshine streaming into the room, they emerged from the soil in numbers, and became very active and excited, a few specimens indulging in short flights. Several were soon pairing; but I was never able, even with the most careful searching, to discover any eggs. Further investigation is therefore necessary before the biography of this interesting little beetle can be fully written.

CHAPTER XX

KEEPERS AND KEEPING, WITH SUB-DIVISIONS DEALING WITH POACHERS AND VERMIN

By Lord Lovat

It is a very common belief amongst moor-owners—tacitly accepted rather than openly confessed—that provided the proprietor is interested in moor management, his keenness in the shooting season, and his intermittent interference at other times of year, will make up for any shortcomings on the part of his paid keeper.

This is, unfortunately, very far from being the case.

Great help may undoubtedly be given by advice and criticism, and the interest of the superior cannot fail to stimulate the keenness of the subordinate. Still the fact remains that however accurate may be the theoretical knowledge of management of the landlord, and however The importance of the keeper. complete his personal attention to the general principles of moor hygiene, the gamekeeper will always remain the executive officer responsible for the thousand-and-one details on which the health of the moor ultimately depends.

In undertaking the management of shooting, it is, therefore, of primary importance not only that a good keeper should be chosen, but also that the terms of his engagement, the nature of his duties, and the extent of the assistance, both permanent and casual, to be given to him should be of such a kind as to give him the widest scope for efficient service.

It is not intended in this chapter to go at length into a description of the methods of selection of a keeper, or the technical details of the duties that he should carry out after appointment. The Committee only desire to suggest a few general principles founded on observations made during the course of the Inquiry, and shown by experience to be established on a strong and certain base.

In the first place it may be stated as a universal rule, and from this

there should be no departure, that the keeper should be the *owner's* and not the tenant's servant. The reasons for this are many, and it would be hardly necessary to go into any of them were it not that this somewhat obvious precept is as often honoured in the breach as in the observance.

Keepers
should be
the owner's
servants.

A tenant, from the very definition of the term, is an individual possessing but a temporary interest in the moor he rents. The tenant's keeper also, whose arrival and departure synchronise with the period of his master's lease, naturally looks to his immediate superior's interest rather than to the future welfare of the estate, or of those permanently connected with it.

In cases of Grouse moors where the heather is well burned, where there are no troubles connected with rabbits, sheep stock, or rights-of-way, and where, broadly speaking, the interests of both contracting parties are identical, difficulties may not occur; but this satisfactory state of affairs does not always exist.

On a badly burned moor, with large tracts of rank, overgrown heather, it is difficult to see how the immediate interests of a progressive landlord and those of a shooting tenant on a short lease can ever be made to coincide.

If the landlord knows his own interests, his first object must be to burn big stretches of stick-heather in order to get the moor into a proper rotation of burning. The tenant, on the other hand, should he be equally well informed, knows that though such heavy burning may be beneficial to the moor in future years, the resulting crop of edible heather will not be increased during his occupancy.

Conflict of
interests
between
landlord
and tenant.

The keeper, therefore, who burns in the tenant's interest will burn in the smallest patches, not in order to increase the food yield so much as to provide basking ground for the old birds, and drying ground for the young chicks. He will leave severely alone the big blocks of old or dying heather, for on these he depends for cover for the stock of birds which happen to be on the ground, their prospective food value not being his concern. This method of heather management, though suicidal, is by no means uncommon, and instances could be given in Scotland and England of magnificent moors on which no long heather is being burned, and which at the end of the current leases will show a decrease of 50 per cent. in value, and that for many years.

Another reason why the tenant should not directly employ the keeper is

that the former is, as a rule, but an autumn visitor. Though his trust in himself be great, and his experience of shooting not small, his knowledge is but too often confined to the months when the heather is in bloom, and the climatic conditions are at their best. He may never have visited the ground during the late winter and early spring months, when the food is short and when the results of moor management are put to the test.

The tenant's knowledge of keepers and their duties is also apt to be perfunctory. A little keenness at shooting time, and a few excuses on the plea of a wet nesting season or bad weather for heather-burning, are quite enough to satisfy the average tenant that every effort has been made to get the best possible results from the moor. In this way the inefficient escape dismissal, and the specious are awarded undeserved praise.

When the keeper is the landlord's servant a very different state of things exists. In the first place, the supervision is continuous and not intermittent. In a year with a short burning season, the foresters' staff, the shepherds and the labourers employed on the estate can be turned on for a few days' burning; draining can be done under an expert sheep-drainer, and the estate *personnel* and organisation utilised without incurring additional expense. Again, in dealing with grazing tenants, the landlord's keeper gets more effective support from the agent, and has the minor difficulties arising from sheep gatherings, dippings, etc., more satisfactorily settled than if the arrangement has to be made through a third party or by a stranger.

This question of the relations between the gamekeeper on the one hand, and the agricultural tenants and their employés on the other, is one to which it is impossible to attach too much importance. The efforts of the most efficient gamekeeper may be nullified by the spite of a hostile farmer or shepherd, while, should a good understanding exist, it will be found that the interests of the moor are studied by all, and that every shepherd is a self-appointed watcher, and not infrequently the best informed man about the moor.

Without dwelling further on this aspect of the question, it may be said that whether from the point of view of management, supervision, or outside help, grave risk is incurred, and no advantage gained, by the transfer of the keeper from the landlord's to the tenant's service.

As to the exact terms of service, no general rules can be laid down. Wages differ in different parts of the country according to local customs, cost of living, etc. It may, however, be stated that it is a good policy to pay keepers a fair living wage, not only with a view to securing good men, but also to let them realise that their services are appreciated, and that they have a billet which it is worth their while to keep.

Zeal may be further encouraged by periodically increasing the wages of a keeper who by his personal efforts has improved the value of the shooting under his charge. When this policy is adopted the criterion should be the net improvement over a term of years, and not the chance bag of one lucky season.

Though the rate of wages may vary with local custom and individual largesse, there can be no doubt on one point, viz., that the emolument should be in "coin of the realm" and not in "kind." Payment in kind not recommended.

The keeper should be a keeper "first and last and all the time." In England a garden or the grazing of a couple of cows may be a desirable addition to wages; in the Highlands a small croft may be a necessity; but in either case agricultural enterprise should be kept down to the margin of personal comfort, and not regarded as a substitute for wages, nor should it be allowed to afford a separate means of livelihood. The keeper's place is on his beat, and not at the market-place watching the sale of stock. Above all things a keeper should have no interest in the sheep grazing on his beat. A man cannot serve two masters, nor should a keeper practise his retriever in herding a ewe stock, or keep his nesting ground quiet by pushing up the lately returned winter "hogs" to the high ground.

Many employers prefer their keepers to be married men, and there is much to be said for the preference. A married man is less dependent upon his neighbours for society than a bachelor, and so can go about his business without attracting attention; for the same reason it is often better for a gamekeeper's house to be situated some distance away from other habitations.

In addition to the adequate payment of keepers, the establishment of a pension fund is a question well worthy of consideration. There is a Scotch maxim, "A stout heart to a stae brae," and a servant who has to get his beat burned in the short time available in autumn

Pension list.

and spring, hunt up his assistants and keep them employed, watch his moor when poaching is probable, be at his master's command early and late, and at the same time look after his traps, must be a man in the full vigour of life. Hardy as the race of keepers is, the time must come when retirement falls to the lot of even the most resolute.

There is no objection to the head-keeper being a man of mature judgment and of riper years. The very fact that he has reached a time of life when he realises that he is unable to do all the work himself, will make him delegate his command, and by increased attention to his subordinates see that the work of all is efficiently carried out. For the under-keeper who has neither the grit nor the brains to climb to the top of his profession a change to some low-ground beat or to the gate-keeper's lodge will often quickly repay the cost of transfer.

There is some difference of opinion as to the number of under-keepers required for a given area of Grouse ground. Speaking generally, the Committee hold that

many English moors, and most Scottish moors, are under-keepered. This finding may not be readily accepted by the parsimonious, but a little study of the financial aspect may bring conviction. There are many moors of 6,000 to 10,000 acres in extent with one keeper in sole charge. An area of this size can hardly be looked over every week, far less trapped, burned, and watched by a single man. On many such moors even one section of 1,000 acres, properly administered, may easily yield a permanent increase of one hundred brace, which, if translated into money value, would represent considerably more than the yearly wage of an under-keeper.

The loss arising from bad or insufficient keeping is often not fully appreciated. A very small number of stoats or hooded crows do an

amount of damage which would exceed the annual cost of an extra hand. If we realise that cases can be quoted where a single pair of "hoodies" have been responsible for the destruction of a hundred eggs, or where individual foxes and peregrines have killed a score of paired birds (equivalent to the loss of fifty brace in the shooting season), it is no exaggeration to say that on good Grouse ground adequate supervision *must* be obtained at any cost. It is difficult to lay down exactly the extent of ground for which an under-keeper can be responsible. This varies with the shape of the beat, the character of the ground, the stock of birds, the quantity of vermin, the amount of night watching required, and

Number of
keepers
necessary.

Dangers of
insufficient
keeping.

the outside duties under the keeper's charge such as rabbit-trapping, low-ground watching, fishing, etc. It may, however, be said that on a hill moor with no low ground one keeper should be able to trap, and with proper assistance to burn, from 2,000 to 4,000 acres.

As to the selection of keepers some owners have a preference for dalesmen, some prefer south country Scots; some, very rightly, have a prejudice against men who have come from a rich man's employ; others will only take men off a moor on which a big staff of keepers is kept. It is ^{Selection of keepers.} difficult to generalise. Good men, like good horses, run in all shapes and from all countries, but it will probably be found advisable, where possible, to take a man who has been "through the mill," who has acted as a kennel-boy under a head-keeper, who is himself a good trapper and an honest man.

Whatever fancies may influence the selection of the keeper the essential qualifications can readily be defined. A keeper must be a good trapper, an observer of natural conditions, and a man with the interests of the moor at heart; above all things, he must be a worker, *not a gentleman who goes to the hill with a gun.*

It is hardly necessary to point out, that when the good man has been secured, he must be kept up to his work by periodical inspection. A check should be kept on the amount of heather burned, the vermin list should be frequently looked over, the number of traps actually *at work* should be ascertained from time to time, if necessary by surprise visits.

To those acquainted with the best type of gamekeeper, it is not difficult to separate the sheep from the goats. The series of disasters which has made all heather burning impossible, the combination of chances which has prevented the traps being set on the day of the inspection, the number of vermin skins that appeared on examination to have weathered more than one winter's storms, the chance which has made the area visited the only badly burned portion of the moor, all afford reasons to show why Napoleon in his wisdom elected to employ excuse-free generals born under a fortunate star. To sum up, a sufficient number of keen young keepers, adequately paid, able to trap, willing to burn, properly supervised by a head-keeper who knows every detail of moor management, should give the required result.

On small moors where only one keeper is employed that keeper must combine the qualities of head-keeper and under-keeper; he must have the knowledge and sense of responsibility of the former with the capacity for

hard work so important in both. Many men of this stamp are to be found, and even if at first a young keeper may be lacking in experience he will soon acquire the necessary knowledge if he is willing to learn, and if his employer is competent to instruct.

Every effort should be made to foster the sense of responsibility in a game-keeper. The importance of this will be admitted when it is considered that during many months of the year the keeper on a Grouse moor is out of touch with his employer, and, if he chose to do so, might leave his beat to look after itself and to become a happy hunting ground for vermin and poachers. Detection of shortcomings is extremely difficult, for no master cares to spy upon his servants, and the sporting department of an estate is seldom if ever efficiently controlled from the Estate Office. Keeness is undoubtedly the basis of the sense of responsibility. If a keeper's whole mind is concentrated upon how best to improve his beat very little training is required to turn him into a conscientious and responsible servant. A young keeper should be given, and encouraged to read, the best books on moor management; he should be made to give frequent reports upon details affecting his beat, both for the employer's information and to help him to realise the many points which require attention. A keeper quickly realises that his opinions are listened to, and is thereby stimulated to experiment in new methods, and attempt to prove their value by definite results.

It is a matter of surprise to those acquainted with sport, many of whom lead an over-busy life in our cities for the greater part of the year, what a number of capable men, intelligent, articulate, shrewd observers, not only of natural history but also of men and matters, are included in the keepers' ranks. There are few owners of moors who have not had the good fortune at one time or another to have men of this stamp in their employment; men who are friends rather than subordinates, with a frank contempt for, or rather a complete ignorance of, the ordinary conventions which restrict the intercourse between class and class. Men of few words in company but with that power of expansion when the audience is congenial, men who are eager to learn and to accept both new views and new facts on every point connected with their profession. It is a real pleasure for any one interested in animal life to take the hill in company with a man of this sort. The habits of the dwellers of the moor, the history of the locality, old-world traditions, the beauty of the surroundings, the customs,

The ideal
keeper.

His per-
sonal
qualities.

habits and idiosyncrasies of the visitors, are commented upon with shrewd observation not unmixed with humour, the whole presented from the detached point of view of the man who is a lover of his profession, who is outside the scramble for preferment, who is satisfied with his position, and does not mean to leave it.

To the really efficient head-keeper the "big shoot" comes only as the crowning circumstance of a busy year. All details have been so carefully prepared beforehand that on the day itself every part of the complicated organisation falls into its proper place at the proper time.¹

His power
of organisa-
tion.

To the master of the art the wind is always in the "air" from which the birds can be most easily manœuvred. Flankers appear by magic in the gully down which, for the first time in the memory of man, the birds have begun to break away. There is an order and bustle about events which acts like magic on the most dilettante breakfast-eater, which pushes on the most grasping of the guns from the "pick up" to the next row of butts, and which even stimulates the gentleman's gentleman to take that extra bag of ammunition which is to help to create the record day.

While the work is proceeding there is no bellowing of forgotten instructions, no downwind drives in which startled coveys and volleys of objurgations hurtle past alternately on a full autumn gale. Drive succeeds drive in orderly sequence. The flickering of a parti-coloured flag, quickly seen and answered by the flankers, is all that betokens the master mind. The birds rise, swing round to the downwind flankers, a sudden display of colour, and in a moment they are over the centre of the line. Little escapes the observation of such a man; even the expert in excuses modifies his usual explanations, the most hardened cartridge burier ceases for a while from his miry operations below his butt.

It is not necessary to dwell on the companion picture. The head-keeper who on the day of the shoot prepares to visit the moor for the first time, the shouting and noise which is supposed to make up for the laziness of eleven long months, the beating of dogs, the coursing of hares, the loud echoes which perplex the under-men and frighten the game, all proclaim inefficiency and generally promise bad, certainly unenjoyable, sport. So much depends on the keeper, not only with regard to the bag to be obtained, but also with regard to the satisfaction of successful manage-

Contrasted
with the
inefficient
keeper.

¹ While making due allowance for the high standard of intelligence required for the successful driving of Grouse it is remarkable how many gamekeepers are not naturally gifted with this particular form of genius. In nearly every case where a gamekeeper is a master of Grouse-driving his efficiency may be traced to the careful training he has received at the hands of an employer who has himself thoroughly studied the subject.

ment the pleasure and interest of well-organised shooting, that no effort should be spared to secure the suitable man.

The keeper's duties in regard to vermin, poaching, control of old heather, and stock regulation are dealt with in other parts of this Report.¹ Certain general rules of conduct are however worth noting.

The first rule to be laid down is that a good gamekeeper should never be idle. It is a fair criticism to make that laziness is the commonest fault in gamekeepers. Also that this laziness in the majority of cases arises from ignorance and not from *malice prepense*.

Many zealous young gamekeepers have been brought up to believe that their whole duties are to burn the heather in the spring, to attend upon the guns in the shooting season, and during the remainder of the year to keep their eyes open, but on no account to disturb their ground. This belief is convenient for the idle, and had its origin no doubt from small shootings, where one man has charge of both Grouse moor and low ground. The sequence of duties on such shootings went on without a break from heather-burning to Pheasant-rearing, and from Grouse shooting to covert shooting; a sufficient round of activity to occupy the keeper's time throughout the year. The arrangement was probably considered satisfactory from the point of view of estate economy, even if it did not give a maximum yield of Grouse.

Where a keeper has charge of Grouse ground and Grouse ground only, a higher standard should be aimed at. He must discard the old belief in an "off season," for the "off season" should be his busy time. He must overcome his dread of disturbing his ground even at the breeding season, for it is then that there is most to be learned as to the nesting capacity of his beat, and the means by which this nesting capacity might be improved. He will not find that the hen bird will desert merely because he happens to have located her nest, whereas if he remains at home one pair of hoodie crows may do as much harm as if he had spent a day walking over the moor and putting his foot on every clutch.²

¹ *Vide pp. 445 et seq. ; chap. xviii. pp. 392 et seq. ; chap. xxi. pp. 454 et seq.*

² Many game preservers will challenge the foregoing remarks as contrary to all accepted theories; but against theory can be put actual experience. One example only need be given:—

On a moor which has come under the Committee's observation, where the annual bag has been known to reach the remarkable total of eighteen hundred brace off 2,000 acres of heather, the gamekeeper in charge by close and constant attention to his duties is able to inform his employer whether it is to be an early or late nesting year, whether the stock is large or small, whether the clutches are above or below the average, and how each beat

While it may be admitted that all needless disturbance is bad it must be remembered that Nature has provided certain safeguards for the protection of the stock at the most critical period of their lives. It is almost impossible to flush Grouse at this season, and one may walk all day over a well-stocked moor without seeing any indication of the presence of birds except by their droppings. Any Grouse that may be flushed are usually cocks or barren pairs, and the sitting hens remain undisturbed though the intruder may pass within a few yards of them.

Certain precautions must of course be observed, the keeper must avoid all noise, and must not return again to the spot when he has marked a sitting bird. He must creep about the moor rather than walk openly, and above all he must not be accompanied by a dog.

There is a growing feeling among moor-owners that closer supervision during the nesting season is desirable, and need not be followed by disastrous results. In another department of game preserving the nesting arrangements of wild birds are assisted by such plans as the so-called "Euston" or "Stetchworth" systems, whereby the period of incubation is shortened by removing the eggs from Partridges' nests and substituting for them other eggs that have been almost hatched under a barndoor hen. The results in many places have been most successful in spite of the disturbance caused by searching for the nests and transferring the eggs.¹

When the keeper has been trained in accordance with conventional doctrines his knowledge of the moor during the nesting season is often very incomplete. He conscientiously marks down some half dozen nests on the edge of the moor, and from these he judges the prospects of the whole ground. If the nests under his observation are flooded out by heavy rain, or destroyed by frost, he reports that the season will be a poor one, whereas if they hatch out successfully his hopes run high, for in his ignorance he does not take into account the distant beat which has been harried by vermin, or the waterless waste in the centre of the moor, where no wise Grouse will select its breeding ground.

It must not be thought that the sole object of watching the stock during

will turn out. This information is obtained by marking any nests that may be found by chance (nests are not deliberately looked for), and by carefully observing the droppings of the "clocking" hens and the young birds. As a rule this gamekeeper and his master form a fairly accurate idea of how the season will turn out even before the dogs are run in July; after this final test it is possible to prophesy the bag with some confidence.

¹ For a discussion of the "Stetchworth" and other methods of Partridge preserving see Teasdale-Buckell, "The Complete Shot," pp. 246-256.

the nesting season is to form an estimate of the shooting prospects, though as will be shown later an early knowledge on this point is of primary importance in regulating the stock. The foregoing remarks are intended merely to emphasise how closely a keeper may keep in touch with his duties without unduly disturbing his ground. In the performance of these duties many practical benefits result. The observant keeper will first of all note which areas are most favoured by nesting birds, and will try to discover what are the particular conditions which may be profitably introduced in the less favoured areas. Some of the favourable conditions may arise from the configuration of the country, a sunny exposure, good natural drainage, shelter from the coldest winds, etc.; but many may be reproduced by artificial means. Natural drainage may be to some extent replaced by carefully constructed artificial drains, the patent dew-pan may be substituted for the burn which has run dry, or a drain and conduits may be constructed to bring a copious supply of running water through the driest parts of the moor. Bad feeding may be improved by intelligent heather culture, gravel may be exposed, or heaps of broken quartz deposited, in the soft, peaty parts of the ground where there is a deficiency of grit; and thus the nesting capacity of the moor may be extended. It may be argued that the Grouse will always prefer to nest in the places which possess good natural conditions, and this is no doubt true; still a season will come when a specially heavy stock has been left, and the possession of a reserve of nesting ground may mean the salvation of a moor which otherwise would become overcrowded.

On his visits of inspection during the nesting season the keeper's hands should never be empty, and his eyes should never be closed to the work to be done, the drainer's spade will be found more useful than the gun, and ten minutes' work will convert a choked-up spring into a clear drinking pool. The dangerous banks of steep-sided drains may be sloped away at suitable intervals, so as to make safe landing stages for any chicks that may be caught unawares by a thunder shower. The fan-shaped morass which spreads down hill from every spouting spring will be tapped at its source, and thus acres of green moss and rushes will be turned again to heather. This will not be the only advantage gained; every stroke of the spade will turn up the grit so often described as "the life of the moor."

There is no room for vermin and an active gamekeeper on the same beat. His constant presence drives away what he cannot destroy, or at least disturbs

the raiders in the prosecution of their designs. The methods of trapping or otherwise destroying vermin are dealt with in another part of this chapter, and here it is only necessary to say that whenever the keeper sees a fox or a stoat or a hooded crow upon his ground he should never rest until he has made an end of it. Every addled Grouse's egg should be given a chance of retrieving its failure by becoming the death-meal of some mountain robber. A keeper should be judged by the paucity of vermin to be found upon his beat, not by the total number he can kill each year.

Destruc-
tion of
vermin.

During the hatching season, and until the young birds begin to fly, the game-keeper may continue to watch his growing stock. About this time also he may employ himself upon the building up of Grouse butts and the bushing of wire fences with bunches of heather. In June and early July much can be done to increase the heather area by the destruction of bracken, which on many moors has monopolised the sheltered glens, and is rapidly encroaching on the hill ground. Bracken can always be weakened, and sometimes even exterminated, if cut over twice a year in the early summer when the tender young fronds are beginning to appear above the ground, and many cases are recorded where Grouse ground has been reclaimed from this noxious weed by the energy of a determined keeper aided by a temporary staff of assistants.

Building
butts: bush-
ing wire.

Destruc-
tion of
bracken.

When the young birds begin to fly it becomes necessary for the keeper to use greater caution in his visits to the moor. He should still keep an eye upon his vermin traps, but he should not leave the roads and moorland paths more than is necessary, and he should avoid flushing the young coveys.

By the end of July he may take stock of his birds with the assistance of his dogs. To ascertain what mortality has occurred since hatching he should count the young birds in every covey, and compare their average number with the average number of eggs which were successfully hatched out. If there appears to be a marked reduction he must try and discover the reason for the loss, whether vermin, climatic conditions, or disease, and if the trouble is local, take measures to prevent a recurrence of the cause in the following season.

Observa-
tion of
stock in
July.

With the shooting season the nature of the gamekeeper's duties become twofold. His first duty is to assist in the destruction of the stock which he has fostered with such tender care, and at the same time he must keep an

ever-watchful eye upon his birds with a view to the continuation of the race into future seasons. With the sporting side of the question we are not concerned, and the practice of stock regulation is dealt with elsewhere.¹ But from the game-preserving point of view it is important that a note should be made of the proportion of old birds to young, of hen birds to cocks, of barren birds to the parents of broods. By a careful comparison of statistics thus collected the gamekeeper may be able to study such important problems of moor management as the following:—The amount of winter stock his ground will carry; to what extent do varying conditions of weather and food affect the proportion of young birds to old; to what extent does the destruction of old cocks and barren pairs influence the number of breeding pairs on his ground. In his investigations into the condition of the birds brought to bag the gamekeeper should remember that the weight of a bird is the best test of health, and he should not scorn the assistance of the spring balance. Everything possible should be done to ensure that all wounded birds are collected and put in the bag, a pricked “piner” becomes a ready victim to disease, and consequently a danger to the moor.

After the regular shooting is over for the season the keeper should, with the permission of the owner, do a little private shooting on his own account, killing down the old cocks whenever he can, either by shooting them down in the green burns or low ground, or by stalking them round the rocky knolls. If too big a stock is left he must get the birds killed in any way that his master will allow.

In September and October in England (and in November in Scotland) he will get his first chance of heather-burning, and thus discount the possibility of an unfavourable burning season in the spring. Doubtless during the season he has marked down sundry patches of old heather which urgently require to be broken up, and he should not feel that the year has been a success unless he has at least endeavoured to reduce these patches to smaller dimensions.

During the winter the keeper's work is less arduous: the stock by this time is packed and strong on the wing; it requires little or no protection—but everything possible must be done to keep it on the ground, and if snow should cover the heather for long periods at a time the keeper must spare no pains with rake and harrow to tide the hungry birds over the time of

¹ *Vide* chap. xxi. p. 454.

privation, and, if necessary, provide them with artificial food and grit. But perhaps the most important duty in the winter is that of vermin inspection. Whenever there is a fresh fall of snow the gamekeeper should be early on his beat to search for the tracks of weasels, stoats, and foxes, and thus he will gain the preliminary information necessary for the destruction of these dangerous pests.

The months of February, March, and April put the gamekeeper's efficiency to the test, for it is principally during those months that it is his duty to provide his stock with food for future years. The good gamekeeper must be a far-seeing man, who, like the forester, lives not merely for the morrow but for the day after, and he must burn his moor with a view to improved results many years ahead.¹

It will be said that the various duties enumerated above represent a far greater volume of work than any man can be expected to perform. It may be admitted that the average gamekeeper is not expected to do so much, but this is rather the fault of the system than of the man, for there is nothing in the foregoing list which may not be overtaken in the course of a year of three hundred and sixty-five days, for even Sundays count where game-preserving is concerned. It is true that for heather-burning, bracken-cutting, and moor-draining the keeper will require temporary assistance; but this assistance should be given ungrudgingly, for the results will yield a handsome return upon the outlay incurred.

Before leaving the subject it is only fair to say that gamekeepers as a class represent one of the finest types of the community; the healthy, open-air life they have to live seems to develop in them the primitive virtues of honesty, loyalty, and content, while the responsibility of their position leads them to exercise their intellectual faculties for the furtherance of the interests committed to their charge. If they have a fault, it is an old-fashioned conservatism, tinged with professional pride, which makes them slow to adopt new ideas; but once they have tested new methods, and found them good, all prejudice is cast to the winds, and they become ardent followers of the cause of reform.

VERMIN AND VERMIN-KILLING.

By a misuse of the term "balance of nature" an argument is upheld in favour of the preservation of birds and beasts that prey upon the Red Grouse.

The game-keeper as a type.
The balance of nature.

¹ *Vide* chap. xxviii. pp. 392 *et seq.*

To speak of a restoration of the "balance of nature" as desirable for the improvement of Grouse moors is beside the point so long as the whole object of every proprietor is to upset that balance in favour of one species only.

How far the destruction of all animals and birds of prey as "vermin" is reasonable, and which of them is most detrimental to a Grouse moor, are questions which should have been settled long ago, yet the discussion as to the use and abuse of vermin-killing has now continued for more than half a century, and still affords ample opportunity to gentlemen of leisure to air their views in the local press.

The controversialists may be divided into two parties. The one, the more earnest and generally the more articulate, argue that to kill vermin is to interfere with the order of creation and to upset the balance of animal life on the moor. They assert that the mortality due to "Grouse Disease" is of man's own making, because by the introduction of protective measures the weak are preserved as well as the strong, and thus the breed is allowed to deteriorate. They contend that if eagles and foxes were allowed to multiply, all the sickly Grouse would be destroyed by them, and only the fittest would survive.

In the other camp may be reckoned those who believe in action rather than in argument, the moor-owner, the sportsman, and the gamekeeper, and it is to these that the present chapter is more specially addressed. There is no doubt that among game preservers, and more particularly amongst gamekeepers, there is a tendency to destroy vermin indiscriminately. The Committee has known a gamekeeper kill cuckoos, and receive so much a head for them from his master because they had barred feathers "like a hawk." Such a master was worthy of such a servant!

Without entering into the polemics of this well-worn controversy a few points not always put prominently forward may be mentioned. In the first place, it may be suggested that owing to the artificial conditions which have for years prevailed on Grouse moors the natural laws have little direct bearing on the point at issue. It is clear that if moor management has accomplished anything, we have long ago passed beyond the limit of stock that the moor would maintain if left entirely to natural conditions. It is reasonable, therefore, to argue, that if we have established and wish to preserve an unnatural stock of Grouse, we must not return to the natural state of things. The practical moor manager is not concerned with

Arguments
in favour of
preserving
vermin.

Game pre-
serving an
artificial
condition.

the laws of natural selection and of the survival of the fittest, but rather with the adaptation of these laws to his own special requirements.

The evidence of history affords a second and equally conclusive argument against the theory that the presence of vermin is conducive to the health of the stock. Written records go to show that even in the eighteenth century, long before game preserving was introduced, Grouse were no less subject to disease than they are at the present day, in spite of the fact that their natural enemies were left undisturbed to keep the "undesirables" in check. As a matter of fact the whole argument is founded on an error. There is no evidence whatever that Nature's so-called scavengers confine themselves to the destruction of the weaklings—their tendency appears to be exactly the reverse. Observation in the field goes to show that the peregrine striking at birds on the wing more often than not picks out the centre bird of the covey, and that the robber of the hen-roost does not take the under-sized pinner, but the fattest bird he can find.

It must, however, be admitted that the keeper who thinks his only concern is to kill all vermin indiscriminately goes equally far towards the opposite extreme. Birds and beasts of prey are not wholly good or wholly bad, in the destruction of mice, rats, and voles they often play a useful part, and the extermination of the greater vermin entails the duty of keeping in check the lesser pests, which might otherwise become too numerous owing to the destruction of their natural enemies.

With these facts in view we may proceed to examine the credit and debit account of the various animals that decorate the keepers' "dulle" tree to see which should be sacrificed in the interests of sport and which should be spared.

VERMIN.

The leading offender amongst four-footed vermin is undoubtedly the fox—difficult of approach, suspicious of the lure, a ranger of miles of country, one day picking a Grouse from the nest, the next day visiting the farmer's poultry yard, taking his meals sometimes off rabbits, poultry, and Grouse, sometimes off rats, voles, or even frogs, his diet must always be described as promiscuous, his morals noteworthy only by their absence. Even in his methods of destruction the fox is guided by no known law;

he will snap off the heads of a dozen fowls without carrying off a bird; at other times he will carefully bury his victims, and as often as not fail to return to their fragrant and probably well-"trapped" remains. Stories are told of the relics of a dozen Grouse killed in the nesting season, and found in various stages of decomposition in or near a fox's "earth."¹

It is easy to see that every effort should be made to rid the moor of an offender with such an established reputation for evil. The methods advocated for his destruction are many, including some of doubtful legitimacy in which strychnine plays a not unimportant part. Of the methods more generally recognised, "trapping" a recent kill, sporing in the snow, watching the den at cubbing time, may be enumerated. In Scotland the "fox-hunter," a gentleman clad not in scarlet but in fustian, is sometimes requisitioned with a mixed pack of lurchers, beagles, and terriers, to aid in the pursuit of his quarry; sometimes he runs the fox to earth, more often he drives him to where a confederate lies in wait to slay him with a shot gun.

Foxes usually travel to a new hunting ground along certain well-defined routes, which from instinct they know to be their appointed path. Keepers are not slow to take advantage of these "trade routes." The mixed pack is laid on to the stale line of a travelling fox at dawn, and the hunters take their posts in well-known coigns of vantage, often with deadly results.

Tom Speedy,² writing in "The Keeper's Book," makes many interesting remarks upon the destructiveness of foxes, and the best methods of reducing their numbers; amongst other devices he quotes that of placing a bait on an island in a pool of water. A road or causeway is formed between the island and the mainland, and on this road a trap is carefully concealed; he specially recommends for bait the carcass of a fox or cat. Speedy, with other authorities, draws attention to the importance of never going near the trap after it has been set lest the fox should scent the presence of man.

The stoat, next to the fox, is the most determined destroyer of game. Living in old stone dykes, disused quarries or cairns, he steals on the unsuspecting Grouse at jugging time—a short worry ensues, and a possible covey is abolished off the face of the moor. It is the habit of stoats to hunt in small packs, and when acting together, and in

¹ In a single day's walk the Committee's field observer found three nests in which the hen Grouse had been snapped up by a fox, leaving the eggs scattered and broken, and a line of hen bird's feathers to tell the mournful tale.

² P. J. Mackie, "The Keeper's Book," 7th ed., 1910: T. N. Foulis: London and Edinburgh, pp. 107-109.

search of food, they are quite fearless, and will let men approach close to them before abandoning the chase. On one occasion the field observer saw a family of seven or eight stoats systematically hunting out a brood of young Grouse while the mother hovered about in a state of great anxiety, running round just out of reach, and trying to draw the marauders away from the brood.

The stoat is a great traveller, and on occasions has been tracked for miles in the snow. Like foxes, stoats seem to follow well-defined lines of migration, and cases are known where keepers have by chance struck upon these lines of march, and have been able to trap many more stoats than were ever bred on their own beats.

The stoat is not, as a rule, difficult to trap. The edge of a dyke, or an opening in a wall, a narrow gully or path between rocks, usually give the best results. His curiosity is often his undoing, and he is, so to speak, his own best bait. When placed in an open run the trap should be covered by a flat stone overlying two uprights. The habit of the animal makes him wish to investigate all objects of interest without attracting attention, and often merely the satisfaction of exploring a partly concealed passage between two stones is a sufficient draw; when the corpse of a dead brother is placed on the flat stone above, the probability of a kill is greatly increased.

Stoats are rarely killed down in sufficient numbers. Like every other kind of vermin they seem to congregate wherever the stock of game has begun to increase; hardly any moor is without them, and a good keeper will kill his thirty to sixty stoats a year, and keep on doing so year in year out without apparently making any impression on the source of supply. The lazy man, on the other hand, has one of two standard excuses which many moor-owners will recognise: on the rabbit-ridden moor — that the stoats confine their attention to ground game; on the moor where there are no rabbits — that there are no stoats. No credence should be given to either statement. Every keeper should have several dozen of the best steel traps (it is useless to employ any other kind) always set and left out on the stoat runs as long as they will spring.

The weasel is very similar in his habits to the stoat. He also hunts in packs, but he is not quite so destructive to game, and feeds more readily on mice, moles, voles, etc.

Weasel.

Amongst other four-footed vermin the wild cat, pole cat, hedgehog, may

be mentioned; the two first named are particularly destructive, but are now so rare that they may be disregarded by the moor-owner. The hedgehog is by no means uncommon on many moors, and is without doubt an occasional egg-stealer. The domestic cat run wild is, of course, a danger, but he is not met so frequently on the open moor as in the hedgerows and coverts near the habitations of man.

The peregrine must be bracketted equal to the fox and the hooded crow in the list of noxious vermin. He is the shyest of all the hawks, and builds in the most inaccessible places; the quickest to kill as well as the readiest to escape with his prey. No British bird has an easier power of flight or more enjoyment in his strength; he seems to revel in his accuracy of eye, and will strike off the head of a Grouse, pass over it, swoop again, and catch the carcass before it has reached the ground. The peregrine kills for sport or for revenge, and will strike down an unoffending crow or jackdaw that has built too near his nest, and not even descend to see where his victim has fallen; at other times he will hunt his terrified victim round and round a glade or corrie, striking over and under until the amusement palls. The peregrine is difficult to trap, no bait will attract him, for he scorns to touch any dead bird or beast which he has not killed himself.

It cannot be argued on strictly utilitarian grounds that the peregrine has much to go down on the credit side; when feeding his young he probably averages his brace of nesting Grouse a day, as the heaps of neatly plucked feathers left on the moor plainly testify. It is hoped, however, that owners of Grouse moors will always leave a few of these beautiful slate-coloured pillagers on some of the wilder and less accessible spots.

For the hooded crow no plea can be made. He is not only the worst but the most widely distributed of vermin. Annually he comes up in his hundreds from his recruiting ground by the sea, and if not watched and destroyed will do incalculable harm both to young birds and eggs. His reputation dates from pre-sporting days. The Celtic name of the bird is "flannag," which means "kill" or "slay." A Morayshire proverb says: "The Guile, the Gordon and the hooded crow are the three worst things Moray ever saw." This is a high testimonial of rascality from a place known to old-time raiders as "The laich of Moray, where all men have their prey."

To see the hooded crow with small beady eye hunt a hillside, drop down beside a pair of Grouse whom he suspects of having a nest, to watch his casual walk round as if merely on a tour of inspection, the fierceness with which he darts at and drives away the pair from their eggs or young, returning again and again until the last of these has been taken, leaves no thought of pity even in the most tender-hearted. The hooded crow usually nests in the birch woods or plantations at the edge of a moor. It is fortunately easy to kill the pair in the nesting season, and they can be trapped with bait at all times of the year. In the nesting season there is no bait like an egg, and even if the "hoodie" does not fall a victim to this bait, it may prove the death of a stoat, a rook, or some other equally objectionable scourge.

Rooks are nearly as destructive as hoodies or carrion crows on some moors, for the supply is inexhaustible, and the nests being at a distance cannot as a rule be destroyed. Rooks.

Jackdaws are often a serious pest upon a moor, and should be kept in check with a firm hand. Their numbers can best be reduced by harrying them in the breeding season. If the old birds are kept off their nests in frosty weather the eggs will become addled. Jackdaws.

An interesting example of the damage caused by jackdaws is furnished by a correspondent of the Committee who rents a moor in Scotland. Before he took the moor the average bag was about sixty brace, and the ground was overrun with vermin, more especially with jackdaws, which nested in the rabbit holes on the hillside. The tenant at once commenced to wage war upon the jackdaws, and offered a sum of one half-penny an egg to any boys who robbed the nests; in each of the last three seasons he has taken over one thousand jackdaws' eggs—one boy alone collecting upwards of five hundred; at the end of the third season the bag had increased to over two hundred brace of Grouse, while a large breeding stock was left. The jackdaws' eggs were found very useful for feeding young pheasants.

Ravens are already so persecuted by the shepherds that they hardly count, though there are still a fair number to be found in the remote fastnesses of the Scottish deer forests. Ravens.

The golden eagle is too noble a bird to rank in the list of vermin. He occasionally kills his Grouse on the wing, but feeds for choice on hares, with an occasional deer - calf or lamb for a change of diet. In former days, when eagles existed in large numbers in the Highlands, their Golden eagle.

depredations were so serious as materially to interfere with sheep farming. The eagle cannot be said to be a desirable recruit to the ranks of the flankers in a Grouse drive; although he not seldom takes on himself this duty, to the rage of the keeper and bewilderment of the birds.

Hawks. Of the hawk tribe all are occasionally destructive; but it must not for a moment be supposed that all should therefore be destroyed.

The kestrel or wind-hover probably does more good by killing mice and rats than he does harm by the destruction of a few young Grouse. The buzzard confines himself almost entirely to small birds, carrion, and ground game.

Gulls. The greater blackback gull is destructive both to eggs and young birds, and should not be allowed to infest any moor on which it is intended to preserve a stock of Grouse.

The black-headed and common gulls are destructive to eggs in certain localities; this, however, must be regarded as an exception rather than as the rule of their habit of life, for Grouse frequently nest and hatch out their broods in the centre of breeding colonies of these birds.

POACHERS.

It has always been customary to divide poachers into two classes, the professional poacher, who makes poaching a means of livelihood, and the occasional poacher, who only takes game for his own consumption, or to satisfy what is called his sporting instinct—for the property of others.

The professional poacher. The professional poacher is a dangerous and undesirable member of the community, and should receive no mercy. He is generally devoid of all the finer feelings, and his sole object is to enrich himself by appropriating, in the largest possible quantities, goods that are not his. He usually belongs to the submerged class which is recruited from the ranks of those who have gone under on account of their own shortcomings—dishonesty, drink, or congenital laziness.

The poaching community. In certain country towns and villages, especially those occupied by a mining or manufacturing population, poaching is not looked upon as a crime, but as a perfectly respectable and often remunerative means of occupying leisure time. When this feeling exists the task of game preserving is a serious matter, and the preventative measures employed

resemble the *levée en masse* rather than what might be called the keeper's "level of every days' most quiet need."

Fortunately for the owners of Grouse moors it is the exception to find the professional class of poacher a very serious menace, owing to the remoteness of moors from the centres of population. Nevertheless, the armed gangs do occasionally turn their attention to Grouse, as may be proved by the supply of freshly killed birds that appear in the windows of the poulterers' shops on the morning of August 12th, earlier than could have been possible had they been killed in the ordinary course of sport.

Systematic poaching of Grouse for the market is less common now than it was in former years. The increase in value of Grouse moors has led to more careful watching and to more severe prosecution, the proprietors in the principal game-preserving counties have in many cases combined together to form associations for the protection of their sporting rights, and the duty of bringing the wrongdoers to justice has been entrusted to competent men. The habits of the Grouse, too, have changed in recent years; whether owing to the introduction of driving or because of the destruction of birds of prey, Grouse are much wilder at the beginning of the season than was formerly the case, and on many moors will not sit to dogs at all.

Twenty years ago it was not uncommon for the poacher's gang to spend the nights of August 10th and 11th hunting the moors with a steady close-ranging pointer. Sometimes it is related that a lantern was suspended from the neck of the dog in order that his movements might be followed in the dark. On obtaining a point the poachers would make a detour, and would gently draw a net down wind towards the dog and drop it over the covey. These nets were sometimes captured, and may still be seen hanging as trophies on the walls of some of the shooting lodges in the North: they are beautiful pieces of work, usually made of silk, very light and very strong.

The only time when Grouse can still be poached with ease is towards the end of the season when they pack and flock to the low ground to feed on the corn stooks. On these occasions they may be snared by horsehair nooses, and there is no doubt that in certain districts this form of poaching is carried on. As the majority of "corn-feeders" are young birds, this form of poaching is specially harmful to a moor. There is no excuse

Grouse
poaching
not general.

Improve-
ment in
protective
measures.

Grouse
poaching
in former
days.

Snaring
on the
stooks.

for the gamekeeper who permits it. The cornfields to which the Grouse resort, and the hours at which they feed, are perfectly well known, and it is the duty of the gamekeeper to be constantly on the spot.

The subject of poaching cannot be considered complete without some reference to the pastime of "Grouse-becking" as practised in the north of England. Becking has already been mentioned in another part of the Report,¹ and the manner in which this habit of the bird has been utilised by poachers is graphically described by the Rev. H. A. Macpherson in the Fur and Feather Series.²

Occasionally the professional poacher goes alone and boldly carries a gun. This method is common in the extreme north of Scotland, where the daylight is of such long duration that it is almost impossible for the gamekeepers to be always on the watch. It is a well-known fact that in flat, featureless country it is very difficult to detect a man upon the moor, or to hear the sound of a shot.

All professional poaching might be prevented if the sale of game by unauthorised persons were discouraged. Game-dealing licences are granted far too often to small country tradesmen, who are prepared to act as the receivers of stolen goods. This might be avoided by granting only a limited number of licences in every town, and only granting them to responsible persons. The licensed game-dealer is supposed to ascertain that the vendor had come by his game honestly, but the law in this respect is seldom enforced.

The occasional poacher. The occasional poacher is a nuisance, and requires careful watching, but it is doubtful if his depredations ever materially affect the stock upon a moor—one pair of hoodies, or the mildest attack of disease, will do more to damage the season's prospects than a score of crofters who take an odd Grouse to give a flavour to the broth.

Though the occasional poacher may not do much harm he must not be encouraged, he disturbs the ground, and wounds more than he kills; too often he is tempted by success to join the ranks of his professional brethren.

No one can deny some measure of sympathy for the small tenant trying to earn a scanty living on a poor hill farm or croft, who finds his stooks of corn in October or November black with Grouse. The crop may be well-nigh worthless, but that makes the temptation all the greater to try

¹ Chap. ii. p. 21.

² Fur and Feather Series, "The Grouse," pp. 65-72.

and get some benefit out of a disastrous harvest. The landlord should deal with such cases in a broad-minded spirit, his gamekeeper should be instructed to assist in keeping the birds off the corn, and any old cocks that he may shoot should be given to the tenant as a *solatium* for damage done.

One form of poaching remains to be mentioned, namely, the catching of live birds and the stealing of eggs with a view to selling them for the restocking of other ground. Catching Grouse alive is perfectly legitimate where a man nets only the birds bred upon his own moor, or on a moor which he has rented for the purpose, but in some districts in the north of England, notably in Cumberland, the practice has developed into an abuse. It is a well-known fact that certain small freeholders on the edge of the hill land who have no Grouse of their own take a heavy toll of the birds which visit their ground from neighbouring moors.¹ An example of the damage done is furnished by one of the Committee's correspondents, who writes as follows:—"Owing to the present system of netting on small holdings, Grouse preserving in Cumberland is a snare and a delusion. To give an instance—my moor in the neighbourhood of —, of about 3,000 acres, used to give a yearly bag of about eight or nine hundred brace and was worth about £500 a year to let, now two or three hundred brace, all shot in the first fortnight to save them from being caught in nets, with a rent of about £100 a year, represents the present return." The only method of checking this evil would be for purchasers to agree to boycott all sources of supply that are open to suspicion.

Netting
live Grouse
and egg-
stealing.

Egg-stealing is not a very common form of poaching; Grouse eggs travel badly, and the advantage of introducing fresh blood by the importation of eggs has yet to be proved.² The practical difficulties also are considerable.

¹ The following passage is worth quoting: "The cause of offence may be only a tiny strip of some pasture, heatherless, Grouseless, perhaps not worth sixpence an acre for any purpose but one. Its want of food and shelter may be so evident that birds seldom light on it, but they have to fly over it, and nets judiciously arranged and managed will, in the course of a season, capture a very large number of them, and do very great harm to the adjoining beats." G. W. Hartley, in "Victoria History of the Counties of England, Cumberland," edited by James Wilson, M.A., vol. ii. p. 439. London: Archibald Constable & Co., Ltd., 1905. *Vide* also Fur and Feather Series, "The Grouse" pp. 76-77.

² *Vide* chap. xxi. pp. 477-479.

CHAPTER XXI

STOCK

By Lord Lovat

THE subject of Grouse stock management is a difficult one on which to generalise, owing to the varying conditions which affect the Grouse in different parts of the country. The question is, however, of so much importance that it is necessary to attempt to lay down certain rules that are generally applicable, and at the same time to note the exceptional cases to which these rules do not apply.

The management of stock.

The first question which naturally presents itself is, What is the ideal stock which good Grouse ground should be capable of carrying?—in other words—how many birds can be supported upon a given area of good heather? Simple though this problem appears, a little consideration will show that no solution can be put forward applicable to all moors. It must be remembered that the number of birds varies with the locality, the heather, the climatic conditions, and migration. Also that even on any given moor the number is not constant, but alternates in succession with the autumn, winter, and spring seasons.

The ideal stock.

Before entering into the conditions which govern and limit the number of birds, and before describing the measures which are recommended to keep the stock on a moor inside the margin of safety, it will be necessary to define the position more accurately by stating—

- (1) Exactly what we mean by the word "stock."
- (2) Certain statistics, from which broad general laws can be deduced, applicable to specific areas of moorland.
- (3) Certain facts and figures gleaned from the records of individual moors.

Meaning of term "stock."

The term "stock" of a moor is used indiscriminately to mean both the number of birds on a moor in summer when the coveys are unbroken, and the number of breeding birds which eke out a precarious living in the late winter and early spring months.

For the purposes of this chapter the term "stock" will be used in the latter sense only.

It has been shown in previous chapters that it is in the early spring that disease invariably appears, it is therefore at that period, and the period immediately preceding it, that the question of numbers is of real significance.

The reason for this is not far to seek; during the months of May, June, and July the fresh young shoots of heather are probably more nourishing than at any other time of the year—even the oldest and most useless heather is not without some food value. In July, August and September berries are added to the Grouse's diet, and in the late autumn and early winter the seed or fruit of the heather is largely eaten. In fact it may be said that from the beginning of May to the middle of the following January the food supply, even on the worst moors, is almost inexhaustible, and during this period the ground is capable of supporting a stock far larger than it could possibly carry during the subsequent three months. If, therefore, a limit of stock is fixed for March and April, it is sufficiently plain that that limit can be carried with safety all through the year.

While it is impossible to give any exact number of pairs of birds that a particular 1,000 acres will carry in any specified district, as this varies with such matters as climate, shooting, etc., it will probably be interesting to many of our readers to learn that, broadly speaking, the number of birds to the acre is curiously constant over wide tracts of similarly situated ground. In Yorkshire and Lancashire there are exceptional moors which carry a pair of Grouse to 2 acres; but in the north of England, generally, one pair to 4 or 6 acres is considered a safe winter stock on *fully-developed moors*. In Scotland the proportion is about one pair to 8 or 10 acres, except on the west coast, where the normal winter stock is often only one pair to 20, 30, or 40 acres. This generalisation can only be regarded as true of the aggregate, and not of individual moors, and it must be borne in mind that the bags obtained will show a much higher ratio. In a normal season the bag will usually be about double the numbers of the winter stock, and in a very good year it may be possible to kill as many as five birds for every nesting pair.

The similarity of results obtained by a comparison of bags on great stretches of moorland enables several important deductions to be made.

- (1st) That there are certain natural limitations, directly connected with the growth and density of the heather crop, which local conditions of climate, soil, etc., enforce in each district.
- (2nd) That while close attention may modify these natural limitations, even the greatest care cannot wholly eliminate them.
- (3rd) That given efficient keeping and supervision, and the control both of sheep stock and shooting, the majority of what are considered third-rate moors might in time be raised to the average of the best of the *similarly situated moors* in the same district.
- (4th) That in any locality, owing to the slow rate at which old rank heather can be converted into good feeding, the progress of a moor from bad to good is necessarily slow.

From the consideration of these generalisations we may now turn to the study of the following records of bags from individual moors which have been selected as typical of each main tract or district.

	No. 1 Moor	No. 2 Moor	No. 3 Moor	No. 4 Moor	No. 5a Moor	No. 5b Moor	No. 6 Moor	No. 7 Moor	No. 8 Moor	No. 9 Moor
Brace	370	576	350	414	1,701	1,319	1,205	250	2,781½	316
"	425	423	472	420	½	758½	67	784	606½	444
"	636	183	560	430	2	716	474	801	913½	683
"	91	315	1,348	611	7½	1,011	1,158½	1,306	1,829½	1,578
"	320	447	80	1,238	265	704½	1,315	692	2,481½	1,674
"	660	704	259	126	810½	465	2,350½	71	4,922½	1,428
"	880	892	411	480	1,774	382	...	72	4,365	885
"	1,214	420	728	1,247	44½	973½	255	250		696
"	...	450	1,643	480	45½	1,261½	886½	1,063		1,361
"	205	780	455	1,267	232	6	476½	2,487		1,540
"	248	1,155	60	160	600	175½	38	5,010		
"	408	1,737		175	572		154			
"	789	529			157		1,268½			
"	1,625	305			236		1,330			
"	80	180			476½		1,010½			
"		370			410		1,184			
"		617			232		395			
"		1,309			303		315½			
"		1,567			146		158½			
"		422			416		429½			
"					785½		528½			

No figures relating to the breeding stocks on these moors are available; but judging from the bags the following deductions may be made :—

No. 1 Moor.—Three hundred to four hundred pair of birds appears to be the limit of stock the ground would carry in March. It will be noted that every time the bag exceeds one thousand brace disaster follows.

No. 2 Moor.—An improving moor apparently able to carry three hundred to five hundred pairs of March stock in a normal year.

No. 3 Moor.—A very typical dogging moor with four hundred pairs of breeding stock a safe limit.

No. 4 Moor.—A small well-burnt moor—note the rapid recovery from disease; also that it is dangerous to approach five hundred pairs of breeding stock.

No. 5a and 5b Moors.—The records begin with the year 1866, and the disastrous character of the outbreaks in 1867 and 1873 are reflected in the bags.¹ The figures in column 5a fluctuate so greatly from year to year that it is difficult to estimate a safe limit for the winter stock—probably about four hundred pairs.

Column 5b represents the bags on the same moor from 1894; in this year driving was adopted as the only method of shooting the ground. The results of better stock regulation under the new conditions are shown by the figures. While there are no individual bags as large as in 1866 and 1872 the average bag has increased from four hundred and fifty-eight brace to seven hundred and six brace in spite of two very bad seasons.

No. 6 Moor.—A breeding stock of about six hundred brace would probably be a safe limit, quite favourable conditions in spring.

No. 7 Moor.—This is a large moor extending to about 25,000 acres, and probably capable of carrying a larger stock than might be supposed from the bags; probably one thousand five hundred pairs would not be too large a winter stock.

No. 8 Moor.—Another large moor, or strictly speaking a collection of moors, on the same estate, extending altogether to 34,000 acres; about one thousand five hundred to one thousand seven hundred pairs would probably be a sufficient breeding stock according to the condition of the heather in the early spring months.

No. 9 Moor.—About five hundred to six hundred pairs.

We find that on each moor so examined there is a very clearly defined limit of winter stock which it is dangerous to approach and almost certain disaster to exceed, and that while in occasional years, owing to unusually favourable conditions, an exceptional stock of birds may be reared, there is a constant tendency for the stock to revert to the normal ratio for the district. The whole art of moor management depends upon a proper appreciation of this tendency, for if the stock be not reduced to the safety limit by artificial means, nature will

¹ *Vide* also p. 477.

inevitably intervene and will regulate the superabundance with such severity that it may be years before the moor recovers.

With these considerations in view we may proceed to lay down the one great law of stock management, viz., *determine the number of birds that the moor will carry safely in March, and irrespective of all other consideration kill the birds down to that limit.*

It is a very curious thing that while all are agreed that stock must be "hammered" in a good year, no real precautions are taken either to find out when a good year is coming, or when a good year has arrived. Nothing is more common than the case of the moor-owner who, after various rumours and counter rumours, at last makes a casual inquiry about Ascot week from his agent or factor as to whether there will be any birds that shooting season. By early July he has settled his Grouse-driving parties, and has selected his shots from his regular autumn visitors, with the sole change of perhaps adding a couple of specially good shots if the report is favourable, or eliminating the names of certain guests in the case of the report not being satisfactory. Towards early August he finds his way on to the moor, and the keeper, who has probably often been found fault with for undue optimism, hints vaguely that there is a "grand appearance," or perhaps, if cautious, "more than the usual stock on the ground." It is not till the first week of shooting that the host at last realises that he has got an abnormal stock of birds. His visitors rejoice, but he himself knows that his prospects of sport for future years are seriously threatened. If he realises the full significance of the position he may attempt to fit in one or two additional shooting weeks late in the season; those who have tried to get together an October Grouse drive will readily appreciate the difficulties of the task. Added to this he may not be favoured by fortune. The earlier shoots may be spoilt by wind or weather, the later shoots may be rendered abortive by the high gales of the equinoctial period, and by the indifferent marksmanship of a hastily collected team of guns. The result is a foregone conclusion. The moor remains insufficiently shot, and by the end of the shooting season no stroke of fortune can avert the risk of disease.

In the case of the let moor in a big year the situation is even more serious. In the first place, the lessee has less favourable opportunities than the owner for obtaining information as to the prospects of the season; in the second place, he has even less chance of killing down his stock if they

are too numerous. He himself is often a fine shot; but the same cannot always be said of his friends. The close-sitting bird of August 12th, or the reluctant "up-winder" in an evening drive, may be killed even by the novice; but once the birds get strong on the wing, or fly with any degree of rapidity, twisting towards the spaces between the guns, rather than following an owl-like course over the centre of the butt, a very different standard of marksmanship is called for. Such birds appear to be immune from all pellets except those in the very centre of the charge. If the lessee does not succeed in thoroughly reducing his stock by early September there is little hope of much being done in the later weeks of the season; he has probably no great acquaintance amongst the "hardy locals," and he will fail to decoy his club friends from London to drive Grouse once the Partridge season has set in.

To avoid this state of things, of frequent, one might almost say regular, occurrence on many moors, it is necessary to adopt certain practical expedients. The keeper should be instructed to get about the moor in the earlier part of the nesting season to ascertain what stock of birds is actually on the ground and whether they are healthy; he should mark down nests on each of the beats, and report by the middle of June how many of these nests have hatched off, and with what results. The Grouse is a particularly hardy bird, and provided that the stock is on the ground, and the eggs have hatched out, it is possible to estimate with some certainty the probable stock which will be available for sport in the shooting season.

Early information necessary.

The modern methods of Partridge management require that the keeper should know not only the number of pairs on each beat, but even the number of eggs laid in every nest. Such accuracy is not necessary for the Grouse keeper. He should have a rough knowledge of the number of breeding pairs on his ground, and from these, by observation of the average yield of marked nests, he should be able to give a shrewd guess of the number of birds that should come to the gun.

Observations of nesting and hatching.

The result from hatchings varies much less than most people suppose. It takes a very bad year to reduce the average yield of a pair of birds below 3.5 of young brought to the gun, and only in very exceptional years does the average covey exceed 5.2 of young birds.

Many keepers will not readily undertake the responsible duty of estimating the probable stock; but it is not really necessary that they should do so for

provided they can supply the facts, the proprietor may make his own deductions, and in any case it is advisable that the keeper's estimates should be checked by his master before they are acted on.

While in England there is some excuse for lack of knowledge of shooting prospects such ignorance is unpardonable in Scotland when the keeper can run his dogs over the moor in July.

When it is certain that a good season is at hand it is probable that not only one moor will be good, but that all the neighbouring shootings will share in the prosperity. It is therefore advisable to pay no attention to the wise men who contend that frequent shooting will tend to drive the birds off the ground, but rather to let shooting party succeed shooting party until the stock of birds has been killed *below the number which is generally left on the moor.*

How this is to be done so as to give the best sport and at the same time the most satisfactory results now falls to be considered.

To enter fully into the respective merits of shooting over dogs and driving from the point of view of sport, is outside the province of this Report.

There will always be those to whom the working of dogs, the study of nature, the finer arts of venery, and the quiet beauties of the moor will provide two-thirds of a day's enjoyment. It is impossible to deny the satisfaction gained from a pair of wide-ranging dogs perfectly trained under a keeper who is thoroughly conversant with his moor, and able to take advantage of every chance of wind or change of circumstance that the day may bring forth. Although the shooting may not be difficult, the surroundings, the assistance which each sportsman is able to give in manœuvring the Grouse, the chance shots which fall only to the alert, the feeling of satisfaction afforded by each old cock that has been outwitted, the short rests, the cool springs, and the cunning cuts from one point to another, all help to make the day's sport difficult to equal, and impossible to beat.

To those who are in the first flight of shots, who love organisation for its own sake, and have the latter-day mania for big bags and pleasures condensed into the shortest possible space of time, driving, on the other hand, will always claim the first place.

It will be readily admitted that there are few more exhilarating moments than the beginning of the down-wind drive, the first half dozen birds neatly killed, the nearest of them lying stone dead 50 yards behind the butts, the

conscious feeling of being able to deal with the situation, and the excitement of watching the big pack neatly turned by the flankers and sailing in serried mass towards the very centre of the line.

While opinions differ as to the pleasure to be derived from either method of shooting, the benefits conferred by each are not hard to detail.

The great advantage of shooting over dogs is that the worst shot should be able to kill without wounding. Dogging where it is possible is an excellent method of regulating the stock in a bad year. It gives an opportunity to kill all the old birds and spare the young. It is possible also to "dog" carefully ^{Dogging.} the outskirts of a Grouse moor without doing any harm to the central beats, and thus provide a means of killing the birds on those parts of a moor which are least effectively driven.

In a good year, dogging is but a very imperfect method for getting on terms with the stock. The mere fact that the coveys are large means that May, June, and July have been dry and fine, that all the birds are from first hatchings, and therefore strong on the wing, and proportionately wild. By the end of the third week of the shooting season if the weather is fine, or earlier if August has been wet and stormy, the birds are nearly unapproachable, and long shots and wounded birds are the chief results of a day's outing.

A further disadvantage of shooting over dogs is that single old cocks almost invariably escape. The walking powers of the parent birds of a covey are limited by the pedestrian ability of their brood, whereas the solitary old bird is subject to no such limitations.

Without going into the details as to how the dogging moor should be worked, certain points may be mentioned which do not always receive enough attention.

In the first place, it may be laid down as a rule—probably an unpalatable one—that in a bad year, when it is desirable to shoot old birds, one gun, and one gun only, should go out with each dogging party. If two guns go together the object of each shooter is to kill outside birds so as not to interfere with his companion's sport: if the shooter goes out alone his object is to kill the first bird on the wing, in nine cases out of ten the father of the brood.

Where dogging is the usual method of shooting the owner should work round the lower fringes of the moors towards the end of the season in order to secure as many as possible of the pricked or badly-feathered birds which have worked their way down to the grassier and wetter ground. In settled weather the high

tops should also be well hunted or even stalked for the old cocks which have resorted to these supposed sanctuaries.

The main advantages of driving are: (1) That it affords a means by which the stock can be killed down to a proper limit; (2) That it tends to mix the coveys, and so prevents inbreeding;¹ (3) That as the old birds are the stronger fliers, and usually lead the packs, it is certain that in the early drives a large proportion of these elderly undesirables will be killed; (4) That provided the host has selected his guns well the death is assured of all solitary old cocks who risk their fortune over the centre of the line.

While these advantages are to be credited to driving, certain items have to be put down on the debit side. Unless the butts are occasionally changed, or the configuration of the ground makes it possible to get all the birds forward to the guns, it is certain that the birds rising nearest to the butts will be more severely shot down than those on the more distant parts of the beat.

All experienced sportsmen have observed that in certain long drives, unless the wind is favourable, a large percentage of the birds first flushed escape to one flank or another, and that only a few come over the guns, while in other drives the birds are flushed from high ground, and, even if they do come forward, are secure from harm, owing to the height at which they fly. The circumstances repeat themselves each time the ground is driven, and become intensified year after year as the birds profit by experience, with the result that on every beat there are certain tracts of ground which form a sanctuary, while other tracts are overshot. It may be said that the overshooting of certain tracts is, relatively speaking, not important, for if one portion is overshot it will quickly be restocked from the other more heavily stocked areas. It is, however, very important that no portion of a moor should be allowed to become a sanctuary, for this will lead to the survival of a race of old and useless birds, and thus reduce the annual yield of the moor.

While driving is advantageous in a good year, it is a very difficult method by which to treat the stock in the years of recovery from disease. In a bad year the host and a few friends may shoot over dogs and agree only to kill old cocks; they will be satisfied with a third of the usual bag if thereby they can bring the moor more rapidly into good order. To ask a party of guns, however, to drive Grouse, and either to refrain from shooting at the coveys, or only to pick out the old birds, is obviously impracticable.

¹ *Vide* note by Mr Rimington Wilson, p. 480.

A great deal has been written, even by those in authority, to the effect that driving *per se* does not add to the yield of a moor. The Committee cannot endorse this view, and in this connection it would not be out of place to trace the history of Grouse driving, and to study the results which have attended its introduction in different parts of the country.

Grouse driving was first introduced in Yorkshire, where, owing to the wildness of the Grouse in that country, it was found difficult to obtain a satisfactory bag by any other means. Naturally the innovation resulted at first in an increased yield, and this gave rise to an exaggerated belief in the merits of driving Grouse as a means for increasing the productiveness of all moors. As a result driving was introduced on many moors where the same conditions did not exist, in other words, when the birds were not so wild as to necessitate this method of killing them. On these moors it was found that driving did not have the same satisfactory results as in Yorkshire, and that in some districts the bags obtained by driving were actually smaller than they had been in the old dogging days.

Effect of
driving on
total yield.

Introduced
from York-
shire.

Driving not
universally
beneficial.

Hence there arose a school of sportsmen who condemned driving as an undesirable institution, and never ceased to lament the fact that moors which were once good dogging moors had been converted into inferior driving moors, for it is well known that once a moor has been systematically driven its value for dogging is greatly impaired.

The solution of the problem is perfectly simple. On all the moors, both in England and Scotland, when Grouse were naturally wild, the introduction of driving was followed by an increase both in the bags and in the stock, for the bags were increased owing to the increased facilities for bringing the birds to the gun, and the stock was improved owing to the possibility of killing off the old and undesirable birds, and leaving the younger and more vigorous to form a breeding stock.

But once the system of Grouse driving had been fully established the improvement came to an end. Moors whose annual yield had been improved by several hundred per cent. ceased to improve when they reached the higher level, for the beneficial results of driving had been exhausted. The question is very fully discussed by Mr Teasdale-Buckell in "The Complete Shot." This writer draws attention to a condition which he describes

Benefits of
driving
limited.

as one of "stagnation," which followed the establishment of Grouse driving. The stocks on many moors had been very much increased, it is true, but were no longer increasing. He quotes the figures from various moors in England in support of his argument, and gives examples of moors in Scotland which have not been improved by the introduction of driving.¹

Mr Teasdale-Buckell seems inclined to think that on the whole the records do not point to any great increase of stock as a result of Grouse driving. He probably does not give sufficient weight to the cases where it was followed by a very marked improvement, for these cases occurred chiefly in England as long ago as 1872 and 1873. He also does not notice that while the introduction of driving in Scotland in more recent years has not had such a marked effect, it has proved an effective method of regulating the stock in "big" years, and has tended to equalise, and, in the main, to raise the average yield on those moors on which it has been given a fair trial.

There can be no doubt that driving has greatly increased the stock of Grouse on practically every moor in England, as may be seen by comparison of the records before and after its introduction. On many moors in Yorkshire, where before the days of driving Grouse had become almost extinct, they are now numerous.

The true benefit of Grouse driving. The beneficial effects of driving at Broomhead are fully discussed in a note by Mr Rimington Wilson, which will be found at the end of this chapter.²

Driving to be satisfactory must be efficiently carried out. It is a *sine quâ non* that good shots must be chosen. Owing to the improvement in guns, and the amount of practice that can be obtained, few sportsmen are so inefficient as actually to miss their bird; but there is a vast difference between the first-class shot who steadily kills four birds out of six, and the indifferent performer who only wounds a similar proportion. Difficult drives, that is to say, drives in which the birds either come at a great height or dip or curve over the line of butts, should be avoided unless masters of the craft are to form the firing line. Butts should not be too far apart—40 yards is a good average distance, and if this be taken as the maximum it will obviate the necessity of firing long shots, and at the same time allow a good performer to finish off the "tailored" birds of his next-door neighbour. The butts should also, where possible, be sunk so

¹ "The Complete Shot," pp. 232-233.

² *Vide* p. 480.

that the birds do not see the guns, and in consequence do not alter the pace and direction of their flight. The expediency of short sky-lines, the disadvantage of having settling ground immediately in front of the butts, the proper use of "hill heads" for cornering the birds, and the general precepts for drivers, flankers, markers, pickers-up, etc., are all important, but do not fall within the immediate scope of this Report.

Though moors should be disturbed as little as possible, it is a question whether the number of driving days on some of the fashionable moors are not being unduly reduced. The rage for big shoots, and the fact that it is difficult to get good shots unless big bags can be offered, probably prevents the full development of the minor driving days, whose main object is the improvement of the moor. On most moors great advantages would be gained by increasing the number of these minor driving days, and this might be done without disturbing the centre of the ground, for the off days might be devoted to the driving of outlying beats and high ground which at other times are never touched.

If then it be admitted that, by means of driving, Grouse may be killed down to the required limit, the question arises as to the exact stock which should be left on each moor.

There are certain general axioms which may be laid down with absolute confidence. The first and most important is that on a badly burned moor, where the supply of good winter feeding is small, the stock to be left on the ground for the winter must be a light one. By good winter feeding is, of course, meant the close grown six-to-ten-years old heather which has already been described in an earlier chapter.¹ Conversely on a moor where the heather has, by dint of severe burning, been brought into such a rotation as gives the largest possible proportion of winter feeding a much heavier breeding stock may be safely left.

On Broomhead Moor, which may be taken as a typical example of a moor where the heather has been systematically burned for many years past, the ground is now capable of carrying a large winter stock without risk. On this moor of 4,000 acres from one thousand to one thousand five hundred brace is regarded as a fair breeding stock from which to obtain a bag of three thousand brace in the following season.

In estimating the number of Grouse that should be shot the bags of

¹ *Vide* chap. iv. pp. 71-72.

previous years should be disregarded; a moor which in the past has yielded an average bag of five hundred brace may in a big year produce one thousand five hundred brace and still be dangerously overstocked. It is *the number left alive*, not the number killed, that should be considered.

It will be urged by many moor-owners that it is impossible to regulate the Grouse stocks with any precision, owing to the migratory habits of the birds. The objection is a pertinent one, and it is this migratory habit of the Grouse which has so often defeated individual efforts at stock management.

It has been pointed out in another part of the Report that in many districts Grouse annually move about in large packs, often leaving the high ground for weeks, or even months, at a time, and congregating on the lower moors.¹ When this occurs it is obviously impossible for a moor-owner to gauge the numbers of birds belonging to his ground which still survive the shooting season, for he may either find that every bird has left the moor, or alternatively that his own home stock is largely augmented by foreign visitors. In the former case it will be impossible to reduce his stock for the birds are no longer there to be shot; in the latter case the packs are usually so large that any shooting that may be possible can make but little impression on the stock. The difficulty is further increased by the fact that it is usually late in the autumn before the seasonal migrations of Grouse occur, often after the close of the shooting season when no legitimate means are available for the destruction of the birds.

Owners have always been ready to admit the principle that there is danger in leaving too large a stock, and some even go so far as to put the principle into practice by instructing their gamekeepers to kill down the Grouse by systematic driving or "stooking" after the regular shooting has come to an end. This practice may result in the reduction of the stocks by a few hundred birds; but is of little practical value unless it be carried out on a large scale throughout a wide district. Other moor-owners adopt a neutral attitude. An owner of a high-lying moor will contend that he has nothing to fear from leaving a large stock upon his ground since the birds will migrate in the autumn to lower ground, when their numbers will be reduced either by shooting or by disease, and thus the stock will be brought to reasonable dimensions before

Difficulties
due to
migration.

A large
winter
stock un-
desirable.

Various
policies
adopted.

¹ *Vide* chap. ii. pp. 25-26.

they return to breed in the spring. The answer to this argument is that if they are to be reduced by shooting it would be more profitable that they should be shot by himself than that they should go to swell the bag of his neighbour; whereas if they are destined to become the victims of disease they may never come back at all, or if they do they may return as a decimated pest-ridden stock, quite unfit for the task of reproducing their species. In the same way the owner of a low-ground moor, where the Grouse have come to winter in their thousands, sometimes argues that it matters little what number of birds may be upon his ground in the winter, since they will return to their own higher moors for the nesting season, and will leave behind them a moderate breeding stock. These owners seem to overlook the fact that the presence of an excessive stock during the winter will most probably result in wholesale mortality amongst those that are left behind however reduced this remnant may be.

The true explanation of the apathy of many moor-owners is that they have not the courage of their opinions. While admitting that in theory it is a dangerous thing to leave a big stock, they know that a big stock may, under favourable conditions, result in a record bag the following year, so they take their chance, unmindful of the risk they run, with the result that a good season which might be followed by another just as good often becomes the starting-point of a series of disastrous years.

It may be laid down as a general rule that it is better policy to aim at a high average of bags, than to attempt to beat all previous records by leaving a large breeding stock.

Stock regulation in a poor season is a comparatively simple matter, and requires but little judgment, no great risk is incurred by leaving the stock untouched, and there is not much temptation to over-shoot owing to the indifferent sport to be obtained upon an understocked moor. Sometimes it is true a moor may be overshot by an undesirable class of yearly tenant who is more intent upon getting value for his money than upon shooting the ground in a sportsmanlike way; but this danger can be guarded against by a strictly worded clause in the agreement. It is only in a "bumper" year that the question of stock management becomes an urgent one.

In places where the migration of Grouse is the rule, efficient regulation is

impossible without co-operation among proprietors. It matters little that one moor-owner should kill down his birds to the limit of safety if there are too many Grouse in the district, for other birds will crowd into his ground from adjoining moors, or his own stock may migrate for the winter to some other district where there is already an over-stock. If, however, moor-owners would combine to reduce the stocks upon their individual moors the whole district would benefit.

Each owner should make it his object to kill down his Grouse until only an average winter stock remains. The task will not be an easy one for in an exceptionally good season it is almost impossible to make any real impression on the stock. There is little risk of over-shooting, for even if a proprietor succeeds in killing every Grouse upon his ground it is quite certain that his neighbours will not be equally successful, and by the nesting season his moor will be more than sufficiently stocked by birds which had been crowded out from elsewhere.

The Committee suggest that where a series of moors adjoin, and where the birds by migration are common in a sense to the whole range, the proprietors, with those of the shooting tenants who grasp the stock problem, should come to an understanding as to the best procedure for their common interests.

It is suggested—

Firstly. That all should agree to get full information as to the prospects of the season at the earliest possible date, either on the lines already suggested in this chapter, or by any other means that may seem best to the individual proprietors or tenants.

Secondly. That at some date early in July the interested parties should meet and agree whether the year is one in which the birds should be (i.) shot in the ordinary way; (ii.) shot heavily; or (iii.) really “harried.”

Thirdly. That arrangements should be made not only to kill down the birds on those moors where they are most plentiful; but to make a point of shooting hard on the boundaries of moors which from slackness or bad shooting are likely to be lightly shot.

Fourthly. That the local circumstances and knowledge gained from past experiences should be made known between moor and moor; that arrangements be made for shooting all high ground specially

hard; that "cheepers" should be universally exterminated; and that the birds should be killed in October and November when they are massed on the low ground.

While the Committee think it improbable that lessees could be got to combine together to shoot lightly in bad seasons there seems no reason why they should not agree to kill the birds hard in a really good year. The majority would welcome the opportunity for making a record bag, while an increase in the number of birds killed would improve the value of the moor to the landlord.

In addition to regulating the numbers of his stock the moor-owner must also consider how the birds may be maintained in health. The practice of shooting down the stock severely whenever the birds show signs of disease has long been regarded as an established rule of moor management; but it may be doubted whether the practice is justified. As a rule when birds are weak and thin at the beginning of the shooting season this is a sign that there has been an outbreak of disease in the spring; but the birds that have survived the epidemic have reached the convalescent stage by August, and should be spared rather than destroyed, for they will probably be completely restored to health by November, and will be valuable as a breeding stock. This subject is fully discussed in another chapter.¹

The case is different when the bird is weak and undersized as a result of being hatched late. The common custom of sparing "cheepers" in order to give them time to develop as the season advances is one which cannot be too strongly condemned, for it is now believed that late hatched birds are a serious menace to the health of the moor.

This real menace has never been sufficiently considered, but would appear to be one of the worst consequences of the loss of first broods, the full result of which is felt far more seriously in the succeeding year than in the season when it occurs. "Cheepers" of August are seriously handicapped for the remainder of their lives. They often apparently come on quickly during the shooting season, but are lacking in bodily vigour and hardness, and compared with the birds that were hatched in May and early June they feel the pinch of winter badly. The hens, exhausted by the double moult and the trials of nesting, succumb in the succeeding spring with untold loss to the moor; the cocks, undersized and badly nourished by the end of winter, die in still larger numbers owing to the exhaustion consequent upon their efforts to procure and to protect their mates.

¹ *Vide* chap. v. p. 128 (also chap. iii. p. 50).

Late broods eventually become the most fertile soil for Strongylosis, which is always potentially dangerous even in healthy birds. This being so, it would obviously be desirable to encourage early nesting, and to save early clutches of eggs from destruction.

There is, unfortunately, no possibility of encouraging birds to nest early unless by artificial feeding on a considerable scale; but at least it is possible to avoid the loss of early nests which is so often the result of burning too late into April. Gamekeepers sometimes speak as though no harm is done if a few early nests are burned over, and as though the second clutches of eggs were every bit as good for the moor as the first hatchings. They may be so far as the shooting of that same season is concerned—with good luck as many birds may be brought to the bag; but for the succeeding season it is likely to be the worst thing that could happen, since it breeds weakly birds that will perhaps manage to survive an open winter, only to disseminate disease in the following year if they do not actually succumb to it themselves.

There are, moreover, reasons, based on actual experience, why second clutches must always produce a smaller proportion of fertile eggs than first clutches. The following account comes directly from a well-known moor proprietor as to the result of hatching three clutches of eggs, each clutch consisting of the first eggs laid by three different hen Grouse. All were consecutively “fertilised” by one and the same Grouse cock. The eggs had thus every possible chance, on the mother’s side, of producing the full number of healthy chicks in every sitting.

The first hen having paired off with this healthy two-year-old cock Grouse, sat and hatched ten chickens out of ten eggs. A second hen then paired off with the same cock, not immediately, but some time after the first hen had begun to sit.

This second hen laid eight eggs, but only four were fertile, and four chicks only appeared. The same cock again, after a similar interval, paired off with a third hen which then laid eight eggs, but not one of them was fertile. Could there be stronger evidence for the superior value of a first clutch of eggs? Under natural conditions the first clutch receives the full value of the cock bird with the best the hen can produce when in her best condition. Suppose that this nest is burned, or still worse, suppose that the hen has been sitting for some weeks, and is then forced to desert by stress of weather or disturbance by vermin. We have now, instead of a half-spent cock with

a hen at her best, a half-spent cock with a hen already exhausted and short of her stock of subcutaneous nesting fat to the extent of several ounces. She has produced seven or eight eggs weighing an ounce apiece, and she now produces half a dozen more. Not only are these six eggs fewer in number than the first clutch, but they are almost certain to be not all fertile. And what is even worse there is the male element to be considered, and if, with the best possible materials in an unspent hen, his second effort at fertilisation is 60 per cent. less efficient than his first, what will it be when he has to deal with the resources of a hen already half exhausted?

The most certain way to avoid disease is to encourage the production of strong, early, robust, well-grown and well-fed birds that can meet and survive the privations of a hard winter, that can, if necessary, fly far afield for food, fight successfully, breed early, moult quickly, and put on new feathers without a check and without exhaustion; such birds, if they are cocks, should weigh from 26 to 30 ounces, should have large red combs, full voices, and thick white-stockinged feet and legs; if they are hens they should weigh up to 27 ounces, should moult rapidly and efficiently almost in midwinter, and after hatching out their broods should be fit to moult again without still showing bare legs and weathered plumage in the shooting season.

And the other side of the question: "cheepers" too small to rise twice on August 12th, hardly three parts grown when the winter is upon them, bare-legged, and with a scanty growth of feathers replacing the chicken "Cheep-down, permanently undersized by the following spring, forced to mate ^{ers.}" with equally undersized fellows on the lower and less healthy beats where the food is soft and the water laden with the unwholesome washings of the hills around; beaten and often killed in their fights for the more desirable mates, they are forced later on to be content with the undesirable. One can imagine such a pair losing its first nest of eggs, and attempting a second. The hen is already a confirmed "piner" exhausted by the production of half a dozen eggs. If she attempts a second brood she is likely to succumb to the intestinal parasites that infest her. At the best, she appears in the August bag as a dull-feathered, shabby, undersized bird weighing 12 or 15 ounces instead of 22 or 24, or she is picked up dead with hundreds of others in April and May as a "piner" which has never bred.

This is no exaggerated picture of the life of more than half the birds

that are sent up for examination as "found dead" or "dying" in the spring, or as having been picked out of the bag in the autumn as unfit for food, or suspected of disease. They are all alike, undersized, poorly - feathered, desperately thin, bare-legged, and badly infested with every form of parasite within and without, and they are in consequence a very fruitful source of parasitic infection to the healthier birds around them, and a fertile soil for the cultivation and dissemination of disease.

The birds referred to are definitely undersized, their bones are small and thin, their measurements are permanently below the average, they have ceased to grow as chickens when their autumn diet became a winter one, and by the end of October, instead of having enjoyed the full and varied supply of the five fattest food months of the year, they have had that of but three or four.

Early hatched birds, on the other hand, are barely distinguishable from their parents by October, or even by September, and when winter comes they are prepared to meet it. They may grow temporarily thinner with starvation; but they can never be undersized.

Another question of importance in the interests of the stock is that of dealing with the old birds.

The following remarks show how poor is the general opinion held concerning the value both of old cocks and of old hens.

Stuart - Wortley in Fur and Feather Series writes: "It is my firm belief that the presence of these useless, and it is no exaggeration to say destructive, birds (*i.e.*, old cocks) has a great deal to do with the scarcity of broods, and the low average of stock to be found on elevated Scotch shootings.

The useless-
ness of old
birds.

"The older birds interfere with the matrimonial arrangements of the younger to the prejudice of the offspring.

"The old barren hens are bad enough, but the old cocks are the worst, and both must by some means or other be destroyed. . . . I would rather poison them than have them on my own ground.

"In the pairing season the old warriors come down from the heights, fight with and vanquish the younger ones, and absorb the young hens; the latter lay nests full of eggs, but they are sterile; while the more youthful and capable cock bird, who would become the parent of a healthy brood, is either driven off the ground altogether, or obliged to remain in a state of combative celibacy.

"The old hen also, who is beyond the age of laying, attacks any young hen who may nest near her, driving her off her nest, thus causing the eggs to get cold, and the incubation to be abortive.

"It is well known that in deer forests where the great object is to get rid of Grouse, the best means to arrive at this end is to leave them alone altogether. The result is that in a great measure they die out; or at any rate their numbers dwindle to the lowest possible point."¹

So also Mackintosh of Mackintosh makes the following statement:—

A "matter of vital importance is the killing down of old cocks."²

"Another trouble results from the presence of these useless old cocks, namely, over-sitting. Probably if one chicken hatches the mother leaves the rest of the eggs, and so though the brood is lost it cannot often end in the bird's death. But when a whole nestful of unfertile eggs has been laid the hen may continue to sit long after the time when a brood of chickens should have appeared, and may even be found on her eggs dead from exhaustion and disease."

All the views expressed above are fully endorsed by the Committee. There is no doubt that old birds are a danger to a moor, and tend to the degeneration of the stock, for not only are they more pugnacious than the younger birds, but they do not produce such large coveys nor such robust offspring.

All moor-owners who take an interest in the improvement of their stock make it a rule to ascertain as nearly as possible the proportion of young birds to old upon their ground, and whenever they succeed in reducing the proportion of old birds the stock is found to improve.

Proportion
of old birds
to young.

One of the Committee's correspondents has made a series of observations upon a moor in Inverness-shire extending over a period of thirteen years. His analysis of the Grouse stocks and relative bags is so interesting that the Committee have obtained his permission to publish it in this Report as an example of how stock may be recorded for purposes of comparison. The analysis will be found on p. 474, and in the letter which accompanied it the following passages occur.

"I now enclose table showing nearly all the information I have as to old and young birds for a series of thirteen years.

"As nearly as possible the moor has been shot in much the same way, and the same keeper has been in charge the whole time.

"An effort has always been made to bag as many old birds as possible

¹ Fur and Feather Series, "The Grouse" p. 148.

² *Ibid.* p. 157.

ANALYSIS OF GROUSE BAG FOR OLD AND YOUNG BIRDS FOR THIRTEEN CONSECUTIVE YEARS.

Year.	How Killed.	Birds Bagged.	Old Birds.	Young Birds.	Ratio of Old to Young.	General Ratio.	Total Bag.	Remarks.	Dogging Results Prior to August 12th.		
									Coveys.	Young Birds.	Ratio.
1897	{ Over dogs Driving	1166 696	458 341	708 355	100 : 154 100 : 105	100 : 133	1862		No	results	kept
1898	{ Over dogs Driving	1098 764	364 310	734 454	100 : 202 100 : 147	100 : 175	1862		No	results	kept
1899	{ Over dogs Driving	966 805	417 325	549 480	100 : 132 100 : 148	100 : 140	1771		No	results	kept
1900	{ Over dogs Driving	782 763	311 413	471 350	100 : 151 100 : 85	100 : 114	1545		No	results	kept
1901	{ Over dogs Driving	870 807	358 377	512 420	100 : 143 100 : 112	100 : 127	1677		128	499	2 old to 3·9 young
1902	{ Over dogs Driving	798 412	378 275	420 137	100 : 111 100 : 50	100 : 86	1210		No	results	kept
1903	{ Over dogs Driving	244 ...	158 ...	86 ...	100 : 55 ...	100 : 55	244	{ Moor covered with ice from June 16th- 19th	Nearly all	barren	pairs
1904	{ Over dogs Driving	651 311	272 143	379 168	100 : 139 100 : 117	100 : 132	962		108	455	2 old to 4·21 young
1905	{ Over dogs Driving	758 573	277 216	481 357	100 : 174 100 : 165	100 : 170	1331		145	793	2 old to 5·47 young
1906	{ Over dogs Driving	1067 896	389 319	678 477	100 : 174 100 : 150	100 : 163	1963		244	1163	2 old to 4·77 young
1907	{ Over dogs Driving	1387 967	479 412	908 555	100 : 190 100 : 135	100 : 164	2354	{ Very wet spring and summer	299	1362	2 old to 4·55 young
1908	{ Over dogs Driving	1368 967	538 412	830 474	100 : 154 100 : 115	100 : 137	2054	{ Snow lay in masses up till May	235	1050	2 old to 4·47 young
1909	{ Over dogs Driving	810 560	307 296	503 264	100 : 164 100 : 90	100 : 127	1370	{ Snow very late on high ground	142	661	2 old to 4·65 young

Remarks.

Since 1904 inclusive, an attempt has been made to run the dogs over every part of the moor prior to August 12th, and the results are registered in the last three columns of above table.

The exact number of barren pairs is not recorded in the figures, but *all* coveys are included.

The whole of the moor is above 1,100 feet over sea level, and the best heather is about 1,200-1,500 feet.

The aspect of the moor is about half south-west and half north-east.

both by selection and by driving all the high ground even above the heather line. Taking the last six years it is curious to note that whereas the state of the moor as shown by dogs prior to August 12th showed on the average 4.68 young birds in each covey, or a ratio of old to young of 100 to 234; the actual recorded bag during the same years showed 100 to 148. The very high proportion of old birds in the bag is, I believe, due to the following causes:—

- “(1) That every effort is made to select old birds in shooting.
- “(2) That the inspection by dogs prior to August 12th does not include *all* the barren pairs.
- “(3) That before the driving takes place the young birds particularly *pack*, and so escape destruction. I have often proved that many packs consist of young hens.”

The analysis is interesting as showing that on the moor in question a larger percentage of old birds is killed by driving than by shooting over dogs; but as the proportion of young birds throughout the season is invariably much smaller than would be expected from the observations prior to August 12th it is possible that the cause of this circumstance is that there has been a general migration of the young birds to lower ground before driving has been commenced. It would be interesting to compare the results of this high-lying moor with similar observations made upon a lower moor in the same district, and thus endeavour to solve the mystery of the disappearance of so large a proportion of the young birds seen at the beginning of the season. On a different type of moor the results would probably be entirely different, thus pointing to the need of adapting the principles of stock regulation to meet the special requirements of the ground.

Many artificial expedients have been adopted for the improvement of Grouse stocks, either by raising their standard of health or in-
creasing their numbers.

Artificial
means of
improving
stock.

Of these the most generally adopted is that of introducing fresh blood by importing eggs or live birds from other moors. It is believed by many moor-owners that by this means inbreeding and the consequent deterioration of the stock may be avoided.

This view raises an interesting point in the natural history of the Grouse.

There is no doubt that on some moors Grouse show a tendency to remain upon the ground on which they are bred, and do not develop the migratory

habits referred to in other parts of this Report. The reason is usually pretty obvious, for it is found that in the districts where the Grouse do not wander in the winter it is because there are no other moors in the vicinity where the conditions will be more favourable than on their own ground. On the west coast of Scotland, for example, owing to the mildness of the climate, the Grouse are seldom driven off the high ground by snow; and on the moors of Yorkshire, though the general elevation may be considerable, there are not the same marked extremes as in the Scottish Highlands. This distinction is well shown by Mr Stuart-Wortley in the Fur and Feather Series, where he gives two sketches to illustrate the difference of conditions in England and Scotland, and in his chapter on Grouse driving he states: "On a Yorkshire moor you are driving *on the tops* all the time. If there is a high point on the moor, rocky and precipitous, it is in extent probably a mere fraction compared with the acreage of good moorland around it. On a Scotch moor you have usually a large acreage above the line of your highest driving ground."¹ It follows that in Scotland the Grouse is forced to leave the high ground in time of snow to seek his food at a lower elevation, and the same motive will cause him to return again in the spring to the fresh young heather on the "tops," whereas in Yorkshire, where the climatic conditions are much the same on every moor, he would gain little by such migration.

Whether migration actually results in a crossing of blood has been often debated. Some naturalists contend that the migrating packs do not interbreed to any extent with the birds upon the moor where they have sojourned for the winter, but that they return to their own ground with their ranks unbroken. The evidence available does not altogether support this view, and indeed it is doubtful whether it is always the same birds which departed in the winter that reappear again in the spring. It is difficult to obtain conclusive proof on the subject, but one or two facts are suggestive. In the first place, it often happens that on ground where there has been a light stock in the autumn, there is sometimes found to be a heavy stock in the following spring, thus pointing to immigration. This circumstance is usually associated with a moor on which the feeding is good. Conversely a heavy stock may migrate wholesale in the autumn, and only a few birds may return in the spring. The reduction of their numbers may,

Does mi-
gration
result in
crossing of
blood?

¹ Fur and Feather Series, "The Grouse," pp. 152-153.

it is true, be due to disease, but is equally likely that the absentees have become naturalised elsewhere.

But the most striking evidence on the subject is furnished by the manner in which a moor, which has been entirely denuded of birds, will recover its proper stock in such a remarkably short time that the only possible solution is the immigration of birds from elsewhere. A good example is furnished by the figures in column 5a on p. 456. On the moor in question the bag in 1866 was three thousand four hundred and two Grouse, in 1867 it was one Grouse. The gamekeeper in charge of the ground gave the following evidence on the subject: "In 1867 there were only about four Grouse left on this moor of 10,000 acres, in 1868 there were only two broods. The four birds appeared to be pined and very weak. I could not make out whether these bred, or whether the two pairs had come from some other place. I would rather say that these birds were so badly affected that it was not possible that they could recover."

Rapid recovery of denuded moors.

Even assuming that the four birds that were left on the ground had been the parents of the two broods referred to, it would have been quite impossible for them to have been the sole progenitors of the large stock which rapidly reappeared and yielded bags of 530 Grouse in 1870, 1,621 in 1871, and 3,548 in 1872. There can be no doubt that the restocking of this moor was due to immigration of birds from elsewhere, and this restocking would have been even more rapid, had it not been that 1867 was a fatal year throughout the length and breadth of the borders, and there were few Grouse surviving in the district. In a "disease" year a moor in the Highlands of Scotland sometimes appears to be cleared of every bird, yet, if the feeding is good, it is fully stocked again within two years.

Result must be due to immigration.

The conclusion is irresistible that, where Grouse are migratory, it is quite unnecessary to use artificial expedients for the purpose of changing the blood. One heavy snowstorm will do more to shuffle the pack than the introduction of hundreds of purchased birds. Moreover, it often happens that imported Grouse do not remain on the ground where they are turned down. Gamekeepers, it is true, will always profess to recognise the foreign strain for many generations by some real or imaginary peculiarity of plumage; it is difficult to verify their statements except by marking the birds, and wherever marking has been resorted to it is found that the imported birds have wandered far afield.

Artificial change of blood unnecessary where Grouse migratory.

Imported birds apt to wander.

In districts where Grouse are not migratory, it is possible that the introduction of foreign birds may be beneficial, and this remark applies in particular to moors which are cut off from other Grouse ground, by arable land or by wide stretches of water. Examples of such moors are the Lomond Hills in Fife, the islands and peninsulas on the west coast of Scotland, the Solway Moss in Dumfriesshire, and Cannock Chase in Staffordshire. But the number of isolated moors is comparatively small.

The success which has attended the introduction of new blood to the Island of Rum is related in Messrs Harvie Brown and Buckley's "Fauna of Argyll and the Inner Hebrides."¹

"In this island, where there is a fair stock of native Grouse, their chances of increase have been much assisted by the introduction of fresh blood both from Meggernie in Perthshire, and from Yorkshire. About two hundred brace have been introduced," and (writes Mr Bullough) "what is remarkable, they assume the characteristics of native birds. One can always get within shot. Is not this remarkable, seeing that in Yorkshire and Meggernie they are so wild that one cannot get near them in winter? (*in lit.* 1889)." And in a later letter it is said (November 1890): "The new blood has done wonders for the Grouse. We could kill six hundred brace any season now, and three years ago the place would with difficulty yield two hundred."

Referring to Mr Bullough's remark as to these introduced Grouse acquiring the habits of the West Country and insular birds of sitting closely throughout the season (the authors) "believe this habit may have rapidly developed from the fact of the birds having realised that Rum is surrounded by salt water, and that a very long flight would be necessary if they desired to migrate; and last, not least, that the abundant heather in prime condition causes them to feel satisfied with their abode. The desire therefore to migrate, or the necessity to seek new pastures, does not exist."

The same authors, in their later work on the Fauna of the Moray Basin,² refer to the danger that attends the indiscriminating introduction of new stock to a moor from a district where widely different conditions may chance to prevail.

In Yorkshire where the Grouse is not so migratory as in Scotland a sufficient

¹ "A Vertebrate Fauna of Argyll and the Inner Hebrides." Edinburgh: David Douglas, 1892, pp. 155 *et seq.*

² "A Vertebrate Fauna of the Moray Basin." Edinburgh: David Douglas, 1895, vol. ii. p. 154.

change of blood is obtained by means of driving, for the packs of young birds are constantly being moved about from one beat to another and get no chance of staying at home on the patch of heather where they were hatched. Thus it would be almost a miracle if they were to seek out and pair with the survivors of their respective coveys, as well as being contrary to the mating instinct of all living creatures. Yorkshire.

Probably this constant mixing of the stock is one of the most beneficial results that has followed the introduction of Grouse driving, and it is principally to this that Mr Rimington Wilson ascribes the large numbers and health of the birds on his Broomhead Moor, for there the Grouse do not migrate nor is fresh blood ever introduced by artificial means.¹

Another method of introducing fresh blood is by changing the eggs in the nests. On some moors this has been successfully accomplished, and it is said that the result has been an improvement in the stock; but the operation is a delicate one and entails a great deal of trouble and much disturbance of the ground. Many failures have been recorded, and the practice is not to be recommended. Egg shift-
ing.

One great objection to the purchase of eggs or live Grouse for the purpose of improving the stock is that it encourages poaching, and it is feared that moor-owners do not always make sufficient inquiry as to whether the fresh blood purchased by them has been honestly obtained.² Objections
to import-
ing birds
or eggs.

It is somewhat surprising that so little has been done in the way of stocking moors with hand-reared Grouse, for Grouse can be reared in captivity almost as easily as pheasants, and it might materially assist the restocking of a moor which had been hard hit by disease if the gamekeeper had a few coops of captive chicks, which he could release as soon as they were old enough to find food for themselves. Hand-rear-
ing.

These minor expedients may on occasion prove helpful, but they are of little real importance when compared with the main rules of moor and stock management. These may be summarised as follows:— Summary.

Ascertain the number of birds on the ground as early as possible.

Determine what stock of birds can be carried with safety over the winter.

Shoot early and often in a good season; shoot old birds only in a bad season.

Regulate the stock by the number to be left on the ground, and not by the bags obtained.

¹ *Vide* p. 480.

² *Vide* p. 453.

Some Notes on Broomhead Moor by Mr R. H. RIMINGTON WILSON.

Having fortunately but little experience of epidemics on this moor, the writer can only approach the question of disease in a negative way, and try to suggest some of the conditions which may tend to make a moor comparatively free from its visits.

In the first place, it may be stated that there has been no serious outbreak here since 1874, but that, before this date, disease in a virulent form attacked the moor on an average once every seven years.

Shooting over dogs was given up about 1870, and the moor was cleared of sheep in 1877.

It may here be remarked that on the first occasion on which a total of over thirteen hundred brace in a day was made on this moor the ground was carrying, roughly, a sheep to 4 acres, and this had been the case for many years.

It is hardly necessary to state that the heather has been burned, and the vermin kept down in the most careful manner, and that the moor in all details has had every attention from a most keen and competent head-keeper. The condition of the moor, however, in all essentials remains the same as it has been for the last fifty years and more. The same head-keeper has had charge of it; no fresh blood has been introduced. No drainage has been done, and practically no alterations of importance have been made. There has been only one radical innovation.

Why then the comparative freedom from disease and great increase of stock on this moor? It can hardly be attributed solely to good fortune.

The writer can only conclude that the answer is to be found in the above-mentioned radical innovation—namely, the peculiar system of driving that has been in vogue here for the last thirty-five years.

The driving of Grouse was of course first adopted as being the only means of making the birds accessible. It was only experience that demonstrated the vast and unexpected benefit to the health of the birds that followed its adoption.

In the same way the Broomhead system of driving the birds backwards and forwards over the same set of butts was initiated as a matter of convenience and facility of transport, and with no intelligent anticipation of the results which the writer feels sure have followed, and to which reference will be made.

The killing-off of the old cocks is usually put forward as the chief reason why a moor benefits from driving. No doubt their destruction is desirable, and

equally so in the opinion of many is the destruction of the old hens. But this is not the main factor of improvement.

The habit of the Grouse left to themselves is to remain close to their early surroundings, and to marry in their own families, with the natural result of decadence and a falling birth-rate.

Driving upsets the family arrangements, mixes all the birds together, and produces a healthier and more prolific stock.

It is often noticed that a good Grouse crop succeeds a severe winter—Nature's method of producing the same result. The severity of the winter causes the birds to shift their quarters, and the all-important crossing of the blood follows; the possible weeding out of the weakly birds helping the general situation.

The system of driving as carried out at Broomhead—namely, over one set of butts—obtains to the fullest extent possible, and intensifies all the benefits to be derived from driving.

The coveys pack, the packs are shuffled and reshuffled till the crossing of the blood is thoroughly ensured—far more thoroughly than under the usual system of driving.

Nor is this the only advantage: apart from gastronomic considerations, it will be conceded that it is of the first importance that the older birds should be killed and the younger left for stock.

It is only the older birds that possess the necessary stamina to be so frequently on the wing and to cross the butts—as they are asked to do—six times in the day. Many of the younger birds soon tire, and finding cover and safety, live to form the nucleus of a young breeding stock.

Another advantage under the above system of driving is that the pick-up of both dead and wounded is almost necessarily a very clean one.

To sum up, the writer believes the freedom from disease at Broomhead for the last thirty years is mainly to be attributed to the fact that the above system of driving, continued for a series of years, has produced a young stock so healthy and vigorous as to be to a great extent immune to disease. The system, in fact, automatically produces the conditions essential to a well-managed poultry farm — namely, young healthy stock and a constant change of blood.

This moor is divided in its lower half by a deep and wide valley, which thirty years ago the birds rarely attempted to cross. That they now require no provocation to make the passage is evidence of their higher physical

condition. There is no possible doubt that their power of flight has much increased in the last twenty years.

The system of driving over one set of butts is suitable, of course, to a very limited number of moors, and even when possible might not be adopted for reasons unnecessary to mention here. The system is mentioned solely as a possible explanation of the remarkable change that came over this moor at a time which coincided with its adoption.

CHAPTER XXII

GROUSE IN CAPTIVITY

By Dr H. Hammond Smith

IN the spring of 1906 the Committee decided to acquire an Observation Area on which experiments as to the origin of "Grouse Disease" could be carried out on healthy Grouse, and inquiries were at once set on foot to find such an area. Reasons for keeping captive Grouse.

The difficulties of finding a suitable place were increased by the fact that it was essential that it should be sufficiently near to London to allow the scientific staff of the Committee to reach it in as short a time as possible whenever necessary. Many sites were inquired about, but all rejected as being too far distant from London. Finding a site. The question of rearing Grouse on this area did not at first arise, and it was only after experience showed that such a thing was possible that the experiment was tried, and a history of the methods adopted, and the experience gained, will be interesting to the readers of this Report.

After much seeking, a suitable place was found in Surrey on the estate of Mr A. Pain, who all through the course of the experiments has shown, by his constant kindness, the interest he has taken in the work. The site chosen consisted of undulating hilly ground with a sandy subsoil Site chosen. covered with luxuriant heather, and dotted over with self-sown pine trees, very like the fringe of many Scottish moors. The special feature which made it suitable for the purposes of the Committee was the free growth of heather of the type most suitable for the food of Grouse. In order to minimise the danger arising from heather fires, Mr Pain has had wide rides cut through his heather—these rides are cut every spring—with the result that there is a luxuriant growth of young heather every summer. This young heather provides excellent food, while the old heather at the edges of the rides makes good cover for the birds during the day.

In 1906 six movable coops of wire netting were made, each measuring 8 feet

long by 4 feet wide, and 4 feet 6 inches in height—this height was essential to allow of the observers getting into the coops when it was necessary to

Coops.

handle the birds; but for those who wish to try the experiment of rearing Grouse for themselves 2 feet 6 inches or 3 feet would be an ample height. The coops were furnished with padlocked doors, and strong iron staples were driven into the ground holding the lower bar of the coop close to the ground; this precaution

Vermin.

is most important as, unless it is observed, small vermin such as weasels and rats would get into the coops and disturb the Grouse. Even with these precautions the Grouse on the experimental area have been much disturbed by vermin, especially foxes, which abound in that part of Surrey; these foxes come prowling round the coops when the birds are sitting, frightening them off their nests. In one case the death of a hen was attributed to a fox frightening her when on the nest, and in her frantic efforts to escape she injured herself against the sides of the coop. Dogs again have been a great trouble, disturbing the birds at all hours by day as well as by night.

Each coop is also furnished with a piece of tarpaulin, which can be used as a shelter from heavy rain or hot sun as required.

At first the coops containing the Grouse were moved on to fresh ground every two days, being placed on the edges of the rides so as to cover about

Position
of coops.

5 or 6 feet of young heather, and 2 or 3 feet of sheltering heather; but later, when the Grouse increased in numbers, it became necessary, on account of the labour involved, to move the coops less frequently, and it was found that moving them once a week was quite often enough. In that case,

Supplying
heather.

however, the birds had to be supplied with faggots or bunches of fresh heather for food at least every two days, and, better still, every day. Later experience has shown that if these bunches of heather are tied in the coops with the tops of the heather hanging downwards the birds eat it just as well, and even better, than when thrown into the coops loose; and the heather does not become soiled by the birds standing on it.

Another important point is the water supply. All drinking water must be absolutely clean, and this has been ensured as far as possible by using

Water.

Hearson chicken water-fountains, which prevent the birds from soiling the water.

In 1906 very few Grouse were received. The results of the experiments on these birds were noted in Dr Seligmann's report. At the end of that season

1906.

four birds were left: of these, two were unfortunately killed by a fox,

leaving two, a cock and a hen, which were in different coops, the hen having been used for a simple experiment. In 1907 the hen began to lay, and laid ten eggs. Then the keeper put the cock into her coop and she laid nine more eggs, but at longer intervals between each egg; out of these nine eggs ^{1907.} she hatched four chickens. The remaining eggs were fertile; but after the first four were hatched she became restless and left the other eggs. Of the four chickens hatched two escaped, and the other two grew up to be about three months old, when they died. This experiment was due to the keeper's initiative; ^{First} but, having ascertained from it the possibility of hatching and rearing ^{chicks.} birds on the experimental area, it was decided that similar attempts should be carried out during the next season.

During the year 1907, thanks to the exertions of those correspondents who kindly supplied the Committee with hand-reared Grouse, far more birds were sent to the Observation Area, and owing to the fact that there was no outbreak of "Grouse Disease" that year, and that no birds were required for experimental purposes by the scientific staff, the Committee had in February 1908 twenty-seven healthy birds: of these two were the old birds ^{1908.} sent in 1906. The remaining twenty-five birds consisted of eleven hens and fourteen cocks. Owing to the cock birds fighting, three were killed during the spring; but precautions were afterwards taken to prevent deaths from this cause. The stock had now increased to twelve pairs of birds, so it became necessary to increase the number of coops. Six more large ones were added, and six smaller ones, which have proved very useful for the segregation of the birds during the mating season and also when the hens begin to sit, for it has been noticed that when Grouse are confined in coops the cocks will not leave the hens alone on the nests but are always driving them about; as soon, therefore, as the hens commence to sit, it is necessary to take the cocks away and keep them in coops by themselves. This year then the Committee had twelve pairs of birds. The hens laid very well, and the experiment was tried of taking the early eggs and putting them under foster-mothers but with fatal results. Two common hens ^{Foster-mothers.} of the ordinary yellow Orpington breed were set on twenty eggs each, and one on seventeen: one hen hatched seventeen chicks and killed them all; the second hen hatched eleven and killed them all; and the third hen ate all the eggs.

Ten young Grouse from late laid eggs were hatched under Grouse mothers, and successfully reared.

In the spring of 1909 a healthy lot of birds were left, and after the sad 1909. experience of 1908 with foster-mothers it was decided to let the Grouse hatch their own eggs. They nested well and sat well; but again the experiment was marred by two misfortunes. One hen was frightened by a fox, and injured herself so seriously in her efforts to escape that she was found dead in the morning, and many of the nests being on low ground were washed out and spoilt by heavy thunderstorms just as the eggs were about to hatch; still eleven birds were hatched and successfully reared. Thus in all, up to 1909, in spite of misfortunes, twenty-three birds had been successfully hatched and reared on the experimental area. And it must be remembered that the work really was experimental in every way, and every credit is due to Parker, the keeper, for the way in which he has carried out the experiments, for he had never seen Grouse till these birds were sent to him, everything had to be explained to him, and the birds were kept under the most artificial conditions possible, both as to environment and climate.

In 1908 and 1909 a number of Grouse were received from correspondents, and during both these years, and especially in 1909, a considerable number of birds were used for experimental purposes. At the end of 1909 it was found that there were more birds left on the Observation Area than the keeper could attend to, and it was decided that if further accommodation could be found some of the birds should be moved. Dr Paterson of the Frimley Sanatorium kindly offered to take charge of some of them, and in December 1909 six cocks and six hens were removed to the grounds of that institution, leaving six pairs on Mr Pain's ground with some birds that were being experimented upon.

The birds that were removed to the Sanatorium were not put on such good ground as at Mr Pain's, and the conditions are far more artificial; but they have done fairly well.

The Grouse on Mr Pain's ground in 1910 were left to hatch out their own eggs, and did remarkably well. The number of chickens hatched is given at the end of this chapter.

With those at the Sanatorium again the experiment has been tried of hatching under foster-mothers, but it has not been a success; not one chicken was reared. If foster-mothers are to be used experiment would show that the ordinary hen is too clumsy; bantams might be more successful.

A second failure with foster-mothers.

The experiment has also been tried at Mr Pain's of mating one cock with two hens; this also has not been a success. At first two hens were placed in one coop with a cock; but it was found that this was a failure on account of the jealousy of the hens, the stronger and more pugnacious hen would never allow the other to receive any attention from the cock bird, and eventually one of the hens had to be removed. But it must be remembered that these two hens were confined with the cock in a small coop, and could not escape from one another; a state of things altogether unlike their natural existence.

Mating one
cock with
two hens.

Another method adopted was that of placing two hens side by side in two coops, and a cock was kept with them and placed in each coop alternately for forty-eight hours. One hen laid seven eggs; the other laid four eggs, but would not sit; the hen with seven eggs hatched one chicken; the four eggs from the other hen were placed under another bird, and all produced chickens.

For the information of those correspondents who may be desirous of rearing or keeping Grouse in captivity, it may be interesting to know how the Grouse have been fed. At first, of course, the feeding was largely experimental: as has already been mentioned the coops were placed where the Grouse could obtain fresh heather for themselves; and it was extraordinary to see the way in which the birds ate the heather. Two birds in forty-eight hours would make the patch of heather contained within their coop appear as if it had been browsed by sheep. Later on the birds were supplied with faggots or bunches of fresh heather, and this was found to answer admirably, for at the Frimley Sanatorium there is hardly any growing heather, and the birds are for the most part kept on bilberry patches, with a few scraps of heather; but they thrive well on their daily bunches of heather. In addition to heather the birds receive a mixture of grain; at first this consisted of dharri, chicken rice, buckwheat, and feed millet; but it was found they did not eat the two last, so now only dharri and chicken rice are given. Experience also shows that Grouse are very partial to fresh vegetables, especially lettuce. Attention has already been called to the necessity of a pure water supply, which is most essential.

Feeding.

Feeding
on fresh
heather.

Grain.

Vegetables.

Another important point is grit. Grouse must have plenty of suitable grit; the best and most natural is white quartz. The Grouse on the experimental area have always been supplied with plenty of this grit through the kindness of Sir Watkin W. Wynn; without this they could not have been

Grit.

kept in health. Grit must be supplied from the earliest stage of the bird's existence; it has been found in the gizzard of a Grouse chick not forty-eight hours old.

When quite young Grouse will thrive on hard-boiled eggs and young heather, but the best food for them is fresh ants' "eggs"; care must be taken not to give the ants as well as the "eggs." The method pursued on the experimental area to get rid of the ants is to put the nest in the oven for a very few minutes; this kills the ants, but does not seem to hurt the "eggs."¹

The birds on the experimental area have remained in splendid condition and plumage. During the four years deaths have been rare among them and have generally been due to accident or misadventure; the old birds of 1906 are still there. Some birds become wonderfully tame, but others seem always to retain their natural wildness; the cocks, as a rule, are bolder, and become tame sooner than the hens. Most of the male birds resent any interference in their matrimonial arrangements, and their resentment is shown in many interesting ways.

On approaching the coops the cocks at once begin to crow, or rather talk; some will mount on the little faggots of heather supplied for food, and strut, and talk, and crow, swelling out their throats, elevating their supra-orbital combs, drooping the wings and fanning out their tails, as if defending their wives—the whole attitude denoting readiness to fight. In fact, one of the birds has been known at the mating time to follow the keeper's wife (to whom he is usually very attached), out of his pen, pecking at her as hard as he could; while the oldest cock of all, usually quite tame, will always attack the keeper if he enters the coop when the hen is on her nest.

As the birds can be observed at a very close distance the plumage can be studied; and the way in which the wings are carried, and the peculiar fan-shaped form of the tail during the courting process, is well worthy of observation.

Mention has been made of the necessity of constantly changing the ground on which the coops are placed; the more often this can be done of course the better for the birds. But it is only fair to say that for the purpose of certain experiments some of the birds were kept on the same ground for months, and it did not seem to do them the least harm; they remained all the time in excellent health and plumage.

¹ Really the pupæ of ants, popularly known as "ants' eggs."

Attention may be drawn to one very important point. It would naturally be thought, that, because the climate of Surrey is warmer than that of the northern parts of the British Isles, where Grouse live in a state of Nature, the Grouse on the experimental area would nest earlier than the wild birds. The exact opposite is the rule; every year it has been noticed ^{Late} nesting. that the Surrey birds lay and hatch later than Grouse in their natural state. There are several reasons to account for this. In the first place, under the conditions existing on the experimental area the birds are artificially and not naturally mated, and this alone may account for late nesting. It is possible, and very probable, that more extended experiments on mating hand-reared Grouse, in the same manner that Partridges are mated in captivity, might lead to earlier nesting; but it has not been possible to make this experiment on the Observation Area. Again the necessity of the constant appearance of the keeper at different times may make the hen more shy of nesting, and the small dimensions of the coops, keeping the two birds always together, certainly is not conducive to privacy for the hen. So that those who try to keep Grouse and rear them on the lines adopted at the experimental area, must not be disappointed at getting late eggs. But, on the other hand, the results obtained on the Surrey area show that it is within the bounds of possibility to keep Grouse in captivity, and to rear from them in such a manner as to enable owners of Grouse moors to replenish by reared birds any loss their moors may have sustained from excessive mortality in a very bad season. Experience shows that it is better to allow the hen Grouse to hatch her own eggs, and not to place them under foster-mothers unless a supply of bantams could be obtained.

Results of the Experiments.

In 1906 two birds were left.

In 1907 by chance four chicks were hatched.

In 1908 tried hatching under foster - mothers and lost fifty - seven chickens and eggs; but reared ten late birds under Grouse mothers.

In 1909 left the Grouse to hatch their own eggs; a thunderstorm spoilt most of the nests—only eleven birds were reared.

In 1910, at Frimley Sanatorium, all eggs under foster-mothers hatched, but the chickens were killed by the hens; probably bantams would be preferable

as mothers, and the sort of bantams that would be most suitable would be "Silkies."

At Mr Pain's ground, where the Grouse were allowed to hatch their own eggs, the results obtained were very remarkable when compared with the results obtained from eggs placed under foster-mothers.

Grouse Hens.	No. of Eggs.	No. of Chickens.
No. 1	7	7
" 2	11	9
" 3	9	7
" 4	7	6
" 5	12	11
" 6	14	{ Put under a foster-mother who ate all the eggs
" 7	7	{ One chicken; other eggs not good.
" 8	4	{ Would not sit; eggs put under No. 5 all fertile.

Hens Nos. 7 and 8 had one cock bird between them. No. 8 would not sit, so her eggs were put under No. 5, and all proved to be fertile, and hatched.

Out of forty chickens hatched out seventeen have died; all the rest of the birds are healthy and strong. Those that died were all between four and six weeks old; these birds were examined by Dr Fantham as well as by myself, and were all found to be suffering from Coccidiosis. Coccidia were chiefly found in the duodenum and blind cæca, but many of these young birds also presented symptoms of pneumonia; in these birds we both found coccidian oöcysts in the trachea, the bronchi, and the bronchioles. It is quite possible that these coccidian cysts in the bronchioles would be capable of setting up sufficient irritation to account for the pneumonic symptoms observed in the lungs of such young birds. It would seem therefore that the old name of pneumo-enteritis, which, as applied by Mr Tegetmeier and others to one of the diseases that caused mortality in Grouse, has met with great criticism, may after all be proved to have some foundation in fact.

CHAPTER XXIII

THE VALUE OF GROUSE SHOOTINGS IN GREAT BRITAIN

By A. S. Leslie

THE Committee have obtained much evidence regarding the value of Grouse shootings both as a form of property and as a means of livelihood to a rural population. Statistics on the subject have never before been collected, and as the opportunity may not occur again the Committee venture to place on record the results of their inquiries.

It is difficult to obtain accurate returns of shooting rents, as the figures fluctuate from year to year in sympathy with the prosperity of the community and the character of the season. There are, however, certain ascertainable facts which make it possible to arrive at a very fair estimate of the average return to be expected, and these facts it has been the task of the Committee to collect and arrange in the form of statistics from which a general deduction can be made.

Grouse shooting is of all forms of sport the most profitable to the general population, it causes little clashing of interests between the sportsman and the pastoral or agricultural tenant, while the policy to be adopted for the scientific management of moorland is equally beneficial to both. It produces a maximum of profit to the wage earner with the minimum of waste, an otherwise unproductive subject is converted into a source of profit, and districts which but for the Grouse would be uninhabited, except by a solitary shepherd, are occupied by shooting tenants and the men employed by them, and the tenure of many small and otherwise uneconomic agricultural holdings is thereby rendered possible.

In connection with all moorland sport one point stands out prominently—the land which is suitable for Grouse is not well adapted for anything else except sheep and cattle. But the pastoral value is in no way impaired by the presence of Grouse, for Grouse and sheep are found to flourish together on the same hillside, indeed the flock-master is often under obligations to the sportsman for the labour which the latter expends upon the burning and draining of the moor.

Grouse shooting—profitable to the community.

Grouse ground of small value for agriculture.

It has been stated that land which is at present given up to Grouse might profitably be reclaimed and utilised for the support of an agricultural population. Experiments have often been made. In the county of Sutherland alone over 100,000 acres were apportioned among an industrious class of agricultural tenants with a view to being brought under cultivation; but the experiment was a failure, and the land gradually reverted to its former state.

The best Grouse ground, that is ground that grows nothing but heather, is always of a poor peaty nature, and is incapable of growing crops to advantage. In this respect it differs from the green land where the soil is rich enough to grow grass and bracken; this green land is of little value for Grouse; but might with advantage be planted with trees or even crops. It is probably true to say that in the selection of waste land for cultivation good Grouse ground is the last that would be chosen by practical agriculturalists.

It is proposed to deal with the present subject under three headings:—

- (1) The direct value of Grouse shootings to the proprietor.
- (2) The direct value to gamekeepers and other employees.
- (3) The indirect value to the community,

Under the first heading the obvious difficulty which presents itself is that of putting a definite letting or selling value upon a given area of Grouse moor. Not only does the yield of Grouse vary considerably according to the district and to the management of the moor, but it has been found that the rents offered for this form of sport depend greatly upon the convenience or amenity of the district. In a district where the scenery is fine, and the climate bracing, a large rent will be readily given for a shooting which in a less attractive district would scarcely command a tenant. It is, of course, impossible to make an accurate estimate of values which depend so greatly upon circumstances and personal taste; but an approximation can be made by dividing the Grouse-producing areas of the kingdom into districts possessing characteristics in common, and in which the average rent is recognised to be at a certain rate for a given average bag. This rate varies between £1, 10s. or even £2 per brace in some districts, down to less than £1 per brace in others.

In each district the average yield of Grouse per acre of moor can be ascer-
Yield of
Grouse for
a given
area.
tained from the annual bags of a large number of shootings of known
acreage. The total number of Grouse killed each year in a given
district may thus be approximated, and the probable rent may be
calculated at the current rate per brace for the district.

The second difficulty in arriving at a correct valuation of Grouse shootings is that in the majority of cases moors are let with houses or shooting lodges, and one rent is paid for both. It is impossible to say what proportion of the rent is applicable to the shooting and what proportion to the residence. The important point to note is that but for Grouse the shooting lodges would never have been built: and if Grouse shooting were to be discontinued the lodges would become vacant, and the outlay incurred upon their construction would be wasted. This being so, it seems right to credit the Grouse with the gross rent paid; but it may be necessary, in order to arrive at the net rent, to deduct a sum to represent interest upon the outlay on building.

A typical example of a moderate-sized Grouse shooting would be one rented at, say, £600 for a period of three months. For this the tenant would probably expect to get, in addition to the shooting, a comfortable house with a garden, and the services of two gamekeepers. The rent might be apportioned as follows:—

Gross rent of furnished house and shootings	£600	0	0
House and furniture valued at, say, £4,000 initial cost—interest thereon at 6 per cent.	£240	0	0
Wages and allowances of two gamekeepers and one gardener, say	150	0	0
		390	0 0
Net rent of shootings above	£210	0	0

The above sum of £210 would not represent the net profit to the proprietor, for he must deduct owners' rates and taxes, wear and tear of house and furniture, value of keepers' and gardeners' houses, cost of stocking the garden, etc. These items would vary according to circumstances, but in most cases it is doubtful whether the net profit from a rent of £600 would amount to more than £150 to £200.

The above estimate is drawn up on the assumption that the Grouse shooting and lodge are to be regarded from a purely commercial aspect as an income-producing subject. But in many cases the house let with the shootings is the private residence of the proprietor, and would have to be maintained in any event, so that the whole interest upon the initial outlays and the expenses incurred for the maintenance of the house and garden cannot form a proper deduction from the shooting rent. In such a case the net profit from the shootings would probably amount to fully one-third of the gross rent received.

From the statistics collected it is estimated that the approximate average yield from Grouse moors in Scotland is about nine hundred thousand brace, and the average rent about £980,000 or, say, £1,000,000, representing a large proportion of the gross income from the ownership of land in the country.

Approximate rent of Grouse moors in Scotland.

In a recently published work¹ the *cumulo* annual rental of Grouse moors in Scotland is estimated at £789,250; but the calculation is based on the assumption that the average rent of each moor is only £250, which is probably too low an estimate.

In England and Wales. In England and Wales the average yield is estimated at three hundred and twenty thousand brace, and the average rent at about £270,000.

Owing to the difficulty of making an accurate calculation of the amount of the deductions referred to, the net rental cannot be very definitely stated; but if it be estimated at one-third of the gross rental it would amount to £333,333 or, say, £330,000 in Scotland and about £90,000 in England. The whole of this sum of net rental must be placed to the credit of the Grouse. It is true that in exceptional cases the residence or shooting lodge referred to might possibly be let during the summer months even without Grouse shooting; but in that case the rent would not exceed £20 or £30 per month, or a total of £75 for three months. Out of this rent the proprietor would have to meet upkeep of house and garden, wear and tear of furniture, and interest on initial outlay. The deductions would amount to more than the gross rent, and the transaction would be unprofitable. In the majority of cases the absence of Grouse would make the shooting lodges absolutely unlettable even at a nominal rent.

It is clear, therefore, that, in the interests of proprietors at least, Grouse shooting is of great importance, and on many estates, owing to the fall in agricultural rents and the increase of burdens, sporting rents form the main source of income.

From the point of view of the employee the question is of equal importance. The census returns for Scotland show that the total number of gamekeepers employed in that country alone is over five thousand three hundred; but of these it is estimated that at least a third are employed upon low ground shootings, leaving between three thousand and four thousand as the number employed on Grouse moors.

Permanent employment.

¹ "Grouse and Grouse Moors," by George Malcolm and Aymer Maxwell. Adam and Charles Black, 1910.

By another process it is possible to make a rough calculation of the number of men obtaining permanent employment upon the Grouse moors in Great Britain. On the smaller moors one gamekeeper usually suffices, but for moors of a greater area than 5,000 acres, or producing a bag of four hundred brace or upwards, it is usually found that a permanent under-gamekeeper is necessary. On the largest moors the number of men employed is smaller in proportion to the area, but on the other hand the rate of wages is higher. Generally speaking, it is found that the ratio in Scotland is about one gamekeeper for every two hundred and fifty brace of Grouse, and in England one to every three hundred brace, so that the number of gamekeepers obtaining permanent employment on Grouse moors would work out at three thousand six hundred in the former country, and one thousand two hundred in the latter country.

After careful comparison of the statistics obtained from every Grouse-shooting district it has been found that the total wages and cash allowances paid to gamekeepers in England and Scotland is about £300,000 per annum, including tips. The details of the calculation are not given as the methods of payment vary in different districts, thus making exact comparison impossible.

Total
wages paid
to perma-
nent game-
keepers.

Indirectly also Grouse shootings are responsible for a great deal of permanent employment. Gardeners, caretakers, and kennelmen are employed in connection with most shooting establishments, and their remuneration must go far to swell the total wage account; but owing to the different circumstances which affect each case, it is almost impossible to estimate the annual wages paid to such extra employees. The addition of £50,000 or about one-sixth to the foregoing wage account would probably not be an excessive estimate, and the resulting sum of £350,000 should fairly represent the total annual wages earned by those who depend upon Grouse shootings for permanent employment.

Indirect
permanent
employ-
ment.

The apportionment of the rent of a Grouse shooting may therefore be roughly stated as follows :—

Net profit to proprietor—about 34 per cent.

Wages to permanent staff—about 35 per cent.

Cost of upkeep, interest on outlay, value of keepers' houses, wear and tear, rates and taxes, etc.—about 31 per cent.

Temporary employment during the shooting season has to be separately considered, for it does not form a deduction from the rent, but is paid by the

occupant or shooting tenant. Such temporary employment consists of the hiring of watchers, Grouse drivers, ghillies, and pony men. The payment received by a highland crofter as a pony man is from 16s. to 18s. a week, and 15s. to 20s. a week for his pony. In Northumberland the hire of ponies is 5s. per day, not including wages of the pony man. The shooting season extends over a period of about three months, and during that time provides well-paid employment for a number of people. The importance of this casual employment may be judged by the fact that in many remote parts of the Scottish Highlands a poor Grouse year, or the failure on the part of owners to let their shooting, results in an addition to the number of those who seek relief from the poor rates.

In England, where practically all the Grouse are shot by driving it is not very difficult to estimate the amount of labour employed. Conditions, of course, vary—on some moors the whole season's bag is obtained in a few days' driving, while on others the ground is driven oftener. But it is not found that this greatly affects the ratio of men employed, for in the former case the number of drivers will probably be larger than in the latter case. Generally speaking, a total bag of one thousand brace may be taken to represent, at least, three weeks' driving or, say, twelve days in all. If thirty drivers are employed each day at an average of 5s. per day, for men and boys the total wages paid would amount to £90, and this figure corresponds very closely with actual experience. From the foregoing calculation it follows that in England the estimated average annual bag would represent over £30,000 paid in wages to drivers. In Scotland it is not easy to estimate the proportion of the bag killed by driving; but, if it be assumed to be one-half of the average annual bag, this would mean over £40,000 paid in wages. When the bag is killed by shooting over dogs the amount paid to ghillies and pony men must be considerably larger in proportion, especially on the west coast of Scotland, where the stock of Grouse is distributed over a wide area, and large daily bags are rare. Then twenty brace per day is considered good sport for a couple of guns, and the wages paid to ghillies and other attendants would work out at an average of over 2s. per brace.

Making due allowance for possible error in the foregoing estimates it will be seen that the wages earned in connection with Grouse shootings must amount to a very large sum each year, and bear very favourable comparison with the net profit obtained by the proprietor.

The indirect benefit derived by the community from the letting of shootings,

though less obvious, is quite as important as the direct benefit. In every country district, both in Britain and on the Continent, the importance of the summer visitor is recognised, and every encouragement is given to the tourist traffic. Railway companies offer special inducements, hotels and lodgings spring into existence to meet the increased demand for accommodation, while landed proprietors and local governing bodies vie with one another to increase the amenity of their respective neighbourhoods with a view to attract the holiday crowd. Tradesmen, job-masters, proprietors, and even local charities, learn to regard the tourist as an important source of income. The value of the shooting tenant from this point of view is not so generally recognised, yet in the long run he certainly brings more money into the country districts than the tourist. To begin with, he usually belongs to a wealthier class than the average tourist, and his requirements are correspondingly greater. He brings with him indoor and outdoor servants, so that a remote shooting lodge may often contain as many occupants as a hotel in a tourist centre. But the principal merit of the shooting tenant is his wide distribution. Many people hardly realise that the regular tourist traffic is confined to a small space along the principal lines of communication and within easy reach of the necessities and comforts of civilisation. In Scotland especially only a very small area is materially affected by tourists and, though the motor car has opened up a number of remote districts where strangers were seldom seen before, these passing visitors are of no benefit to the community until they arrive again at a halting-place upon the beaten track. The shooting tenant, on the other hand, looks for his sport as far as possible from the main tourist routes, and usually at some distance from the centres of population: thus the area which has not been invaded by the tourist is occupied by the sportsman, and neither class interferes with the interests of the other.

Indirect
benefit to
rural
districts.

Many shooting tenants have endeavoured to calculate the indirect expense connected with taking a Grouse moor in Scotland, and the result of their combined experience seems to be that for every pound spent in rent from 15s. to £1 is spent on other expenses connected with the undertaking. In the recent work already referred to the indirect expenses are reckoned as equal to the rent.¹ Under this heading railway travelling, carriage of goods, cartridges, extra wages, dogs, household supplies, hiring and entertaining may be included.

¹ "Grouse and Grouse Moors," pp. 28-29.

Of the above the item of wages to extra keepers, Grouse drivers, etc., has already been dealt with. Many others do not directly benefit the local community, but the most essential of all, viz.—household supplies—^{Household supplies.} of the utmost importance. It is true that some shooting tenants obtain many of their stores direct from London, but, even so, there are numerous necessities of life, *e.g.*, butter, milk, eggs, poultry, forage, meat, fish, mineral waters, etc., etc., which can only be procured upon the spot, and wherever there is a local tradesman within a reasonable distance of the shooting lodge he makes a point of catering for the sporting tenants on such lines as will secure their patronage. Probably more than half the household supplies are purchased in the district. So far as Scotland is concerned the average annual sum so expended would, on the basis of the gross shooting rent, amount to about £225,000, to which has to be added a further sum to include sundry payments for the hire of dogs and their keep, hiring of horses, carriages, etc., carting, and various other incidental expenses. Altogether the indirect benefit derived from the shooting tenants in Scotland cannot amount to less than £300,000, representing the circulation in rural districts of money which, but for the existence of the Grouse, would have been spent elsewhere, or not at all.

In England the indirect benefit derived from the shooting tenant is less than in Scotland, owing to the fact that in the former country many of the moors are shot from a neighbouring hotel or country house, and it is seldom that a shooting party takes up its residence on or near the moor for any length of time. Still even in England incidental expenses are incurred for hiring, hotel expenses, supplies, etc., which might be reasonably estimated at a sum equivalent to 20 per cent. of the gross annual rental, making a total sum of, say, £50,000 spent in the districts.

From the foregoing figures and estimates it will be seen that the value of Grouse shootings as a factor in the national prosperity may be stated in figures as follows :—

Gross rents received	£1,270,000
Gross wages earned	464,000
Indirect receipts by the district	350,000
	<hr/>
	£2,024,000

Large as these figures are, they do not exhaust the list of benefits, for there are other indirect profits which it is impossible to state even approximately in figures. The building, equipping, and maintenance of shooting lodges alone must represent a very large sum paid into the pockets of local contractors and tradesmen.

Building of
shooting
lodges.

Lastly, it must be noted that the Grouse shootings of Great Britain bear a very large share of the burden of taxation. In the sparsely populated Highlands of Scotland the proportion is often very striking, for in some parishes there are no towns or villages, hardly any agriculture, nothing of value but the sheep farms and Grouse moors. In such parishes it is often found that the value of the shootings amounts to one-half, or even three-fourths of the assessed rental. If the shootings lost their value the whole of this proportion would fall upon other interests.

Payment
of taxes.

In "Grouse and Grouse Moors" attention is drawn to the benefits which accrue to the Imperial Exchequer by the issue of game licences, gun licences, and game dealing licences. The total amount of these licences in Scotland alone is stated at £34,166, of which nearly £30,000 is paid for game licences.

From the foregoing brief summary it will be seen that Grouse shootings are an important item in the welfare of the country, and that it would be a serious calamity if anything occurred to impair their value. Yet from time to time legislation has been proposed which would strike a serious blow at this source of national wealth. The Access to Mountains Bill, which aroused so much controversy when it came before the House of Commons, received support from many urban members who did not realise its significance. If in the future any legislation on the subject should be introduced, much harm might be avoided by providing reasonable safeguards. The solution might be found in the multiplication of rights of way, but in return the public should be expected to leave the moors undisturbed during the nesting and shooting seasons, and to refrain from wanton damage.

Access to
Mountains
Bill.

Note on the Management of Sheep Stocks.

The Committee has frequently been consulted by owners of Grouse moors as to the advisability of removing or reducing the sheep stock upon their land, with a view to improving the yield of Grouse. The subject is one on which it is difficult to lay down a general rule, owing to the variety of the conditions in different parts of the country. The following remarks must therefore be

regarded rather as a summary of existing evidence than as an absolute solution of a problem which from its very nature admits of no universal answer.

On those moors which are covered with heather, and which show no tendency to revert to grass, a sheep stock is distinctly beneficial to Grouse, and several moor-owners have informed the Committee that in order to maintain the full stock of birds they have found it advisable to re-stock cleared ground with sheep. The reason for this is not far to seek. The paths and small open spaces made by sheep form excellent drying ground for young birds. The hollows that sheep scoop out for themselves, in dry banks facing the sun, form admirable dusting places for coveys, and often add to the grit supplies of a moor. The heather growth is improved (1) by the sheep eating down the young heather, and so causing it to grow short and thick and form a close dense canopy which helps to resist the ravages of frost in spring; (2) by their eating down the grass; and (3) by their treading the surface of the ground, thus hardening it and preventing the growth of moss. It is also possible that sheep droppings may increase the number of flies and beetles on which the Grouse chicks feed so largely. The very fact that sheep and shepherds are on the moor is apt to be an incentive to extensive heather burning, while their presence acts as a deterrent to poachers.

While all these benefits accrue from moderate sheep stocks, certain disadvantages have to be reckoned with in all cases where sheep are allowed access to a moor.

As has been pointed out in chapter xviii. in the case of old stick heather, the whole growth, and in the case of twenty-year old heather, a considerable portion of the growth springs again from seed after the moor has been fired. The tendency of sheep is to crowd on to the recently-burned patches for the young sweet grasses that grow there. The tender, slightly-rooted heather seedlings are pulled up wholesale and, if the stock of sheep is excessive, it may take years before the heather will once more assert itself as the dominant crop.¹

On land which has a tendency to go back to green ground, the control of sheep stock is an even more important matter than it is on the average heather-covered moor. In this case there is a risk, not merely of the return to heather being delayed, but even of the total extinction of the heather crop. Such extinction of the heather would be against the interests of sheep as well as Grouse, for it is well known that a certain

Sheep ad-
vantageous
on heathery
moors.

Sheep on
grassy
moors.

¹ Vide Pl. LVII.

proportion of heather is an advantage on all sheep farms. Whether the ground which naturally goes back to green ground after burning is more profitably occupied by sheep, or by sheep and Grouse, is a matter which is outside the scope of this Inquiry, and each proprietor must decide the question for himself. If, however, the landowner does wish to keep both sheep and Grouse on his moor, he must make up his mind to one of two alternatives, either to reduce his sheep stock to such a limit as will enable the heather to grow after burning, or to fence temporarily blocks of newly-burned ground.

On the subject of a stock controlled within reasonable limits, very interesting facts have come to the notice of the Committee, and without entering too far into the theory and practice of sheep farming, they feel they have got enough evidence to satisfy themselves that not a few sheep ^{Control of} _{sheep stock.} runs, especially those occupied by a joint stock ("storting" or common grazing), would be benefited rather than injured by close control.

Cases have come under the observation of the Committee, in which lessees of Grouse moors have leased the grazing rights in order to regulate the sheep stock, with the result that not only was the yield of Grouse increased, but also a marked improvement was effected in the health of the sheep stock.

As an alternative to placing a limit on the stock, a practice has been adopted in certain districts in the south of Scotland, of devoting a separate farm or grazing to the ewe "hoggs" and "gimmers" before drafting them into the breeding flock. This class of young sheep, like feeding ^{"Hogging."} wethers, is much less hard on heather than ewes, and there is evidence to show that ground devoted to "hogging," will produce much more heather than precisely similar ground carrying a ewe stock. The practice may be tried as a palliative when the heather shows indications of dying out, but it is doubtful whether "hogging" is possible except on the larger sheep farms of the Borders.

On the subject of fencing newly-burned ground, a good many interesting experiments have been investigated by the Committee. The exact number of years for which it is necessary to fence areas of burned ground, and the size of the patches which it is advisable to enclose (so as to ^{Fencing} _{burnt areas.} keep down expense in fencing, and at the same time not to cut off too large a proportion of the moor from sheep), must be suited to local circumstances. On an average area of hard moor ground where heather of not over twenty years has been burned, three years' enclosure from sheep is sufficient to get the heather seedlings fairly established. In the case of grassy ground, especially

if old stick heather has been burned, this close time must be doubled. It is a mistake to keep the ground fenced for too long a time; the sheep should be allowed to return as soon as the heather seedlings are rooted in the ground, otherwise there is a danger of moss growing up and choking the young plants. It will be found advisable, in order to save fencing, to fence square blocks chosen as a rule on ground which will rapidly come back to heather. Woven fences with iron standards which can be rolled up and shifted on pony back will probably be found to be most convenient. The size and number of the patches will naturally vary with the extent of the moor, and the amount of money that the owner is prepared to spend. It will probably be found better to enclose a few good-sized blocks of 6 to 20 acres rather than a number of small patches. Care should be taken to select the position of these blocks so as to suit the drives on the moor. All wire fences should be carefully bushed with heather, for experience shows that new fences are specially dangerous to the Grouse stock.

INDEX

(Note: "f," "ff" = "following" page or pages.)

- Access to Mountains Bill, 499
 Acclimatisation of Grouse, 1, 2
 Accounts, Abstract of Committee's, ii. 19 ff
Adimonia suturalis, see *Lochmæa suturalis*
 Age, methods of ascertaining, 62, 65, 66
Aleurobius farinæ (flour-mite) on Grouse, 364
 Alimentary tract, parasites in, 325
Amœba lagopodis, 328
 in fæces of Grouse, 328
 staining, 328
 schizogony, 329
 encystment, 329
 pathogenicity, 329
 Anæmia, 118, 269; ii. 107
 Anatomy, normal, 100
 Anatomy in health and disease, 284-285
- BACILLUS COLI*, 200, 276-276
 occurring *post-mortem*, 200
 in liver, 282, 289; table, 290 f
 not associated with mortality, 200, 275, 297
 relation to Strongylosis, 290 ff
 ,, to Coccidiosis, 260, 295-297
 ,, to tapeworms, 293 ff
 Bacteria, carried by coccidia, 260, 295-297
 Bacteriology, methods, 278 ff
 Bantams as foster-mothers, 489
 "Becking," 21, 452
 Berries, as food, 73, 74, 105
 as grit, 98
 seeds as vermifuge, 98, 99, 103
 Bile, cultures from, 280
 Bill, accidental injury to, 168
 Blackgame, grit of, 99
 accidental death, 158-159
 remarkable series of deaths, 158-161
 antagonism to Grouse, 177
 heather beetle, eaten by, 424
 "Blackhead," in turkeys, 268, 329, 330
 Blaeberry, as food, 76
 value of, 412
 proportions eaten, 412
 Blood of Grouse, 308 ff
 cultures from, 280
 observations on, 308 ff
- Blood—*continued*
 methods of examination, 309
 staining, 309
 erythrocytes, 309
 leucocytes, 310
 thrombocytes, 313
 erythroblasts, 314
 effect of helminthiasis on, 316
 ,, of *protozoa* on, 314-315
 ,, of Coccidiosis on, 251
 eosinophilia in, 231, 316
 bibliography, 317
 Blood-counts, 314 ff
 normal, 314
 pathological, 314
 when *Spirochaeta lagopodis* present, 314
 ,, *Leucocytozoon lovati* present, 314-315
 ,, *Eimeria (Coccidium) avium* present, 315
 in helminthiasis, 316
 Blow-fly, see *Calliphora erythrocephala*
 Bolton Abbey Moors, 383
 Bones, fractured and reunited, 153-164
 Bracken, 400, 406, 412
 crofter ponies and, 412
 cutting, 441
 Breeding, risks attending, 181 ff
 by last season's "cheepers," 459
 loss of condition, due to, 471
 Breeding-season
 weather of small importance, ii. 114, 120
 Broods, early, value of, 470 ff; ii. 130
 late, 173; ii. 130
 danger of late, 377, 469; ii. 121
 diminishing value of late, 470
 second, of small value, 470-471
 experiments, 470
 Broomhead Moors, 385, 401
 effects of "driving" at, 464
 breeding stock at, 465
 notes on, by R. H. Rimington Wilson, 480-482
 "Bumblefoot" in Grouse, 170-171
 "Bushing" of fences, 502
 Butts, distance apart, 464
 Buzzard, not destructive to Grouse, 450

- CÆCUM**, 105-108, 116 ff, 286
 importance of, 109
 obstruction of, 115
Trichostrongylus in, 116-117, 286
 normal, described, 287
 diseased, described, 288
 caecal excreta, 107-108; ii. 91
 cultures from, ii. 101
- Calliphora erythrocephala* (Blow-fly)
 as carrier of coccidian spores, 262
- Capercaillie, antagonism to Grouse, 177
- Carron Moor, 387
- Catechu, a specific in Coccidiosis, 269, 271
- Cawdor Moor, 387
- Ceratophyllus gallinulae*, 362
 „ *garei*, 363
- Cestodes, 334 ff
 chemical reaction of media necessary to, 105
 not a cause of "Disease," 193
 intermediate hosts unknown, 369
 development of, 370
- "Cheepers" and late birds, 469 ff
 should be killed out, 469
 liable to "Disease," 471
 fate of, 471
- Claws, as guide to age, 63
- Claw-shedding, 41, 46, 50, 63
- Cobbold's theory of "Grouse Disease," 188 ff, 274, 396
- Coccidiosis, 235 ff
 all "Grouse Disease" Strongylosis or, 204
 may occur in man, 235
 in rabbits, 235, 240, 242 f, 245, 254, 257, 296
 in pheasants, 251
 in fowl chicks, 253, 259, 260, 261
 in turkeys—"blackhead," 268, 329, 330
 in young pigeons, 253, 261
 in canaries, 269-270
 in Grouse, 249 ff
 rarely fatal to adults, 231, 251
 fatal to chicks, 16, 17, 36, 251, 261
 affecting liver, 125, 259
 duodenal, 241, 250
 typhlitic, 241, 250
 confined to digestive tract, 257
 accompanied by anaemia, 269
 symptoms, 249, 254
 effect on weight, 140, 204, 255
 „ on appearance, 255
 in hand-reared Grouse, 490
- experimental studies, 252 ff
 infection, artificial, 252 ff; ii. 103 ff
 „ natural (by water), 252-253, 261
 associated with bacterial infection, 260, 296
 blood-count in, 315
 leucocytosis in, 251, 315
 dissemination by insects, 246, 262
 „ by birds, 268
 „ in dry weather, 263-264; ii. 120
- preventive measures, 266 ff
 burning dead bodies, 251, 257, 267
 heather-burning, 267
 sanitary precautions, 267
- treatment, 269
- Coccidiosis—*continued*
 catechu, 269
- Coccidium (Eimeria) avium*, 235 ff
 habitat, 235 ff, 250
 life history, 247
 synonymy, 236
 staining, 237, 242
 morphology, 237
 sporozoite stage, 238, 247
 trophozoite stage, 239, 247
 schizogony, 239, 247, 250-251, 257
 merozoites, 240, 247-251, 257
 periodicity, 246
 gametogony, 241, 247-251, 257
 encystment, 242
 sexual differentiation, 243, 247
 fertilisation, 244, 249, 257
 periodicity, 259
 sporogony, 245, 249, 250, 260
 onset means recovery or death of host, 260
- oöcysts, vitality of, 263
 effect of moisture on, 263; ii. 130
 „ of drying on, 264; ii. 130
 reagents destructive to, 264 ff
 effect on host, 249
 „ on weight of Grouse, 140, 204, 255
 as inseminating bacteria, 260, 295-297
 insect carriers of, 246, 262
 bibliography, 271
- Coccidium cuniculi*, see *Eimeria stiedæ*
- Coccidium oviforme*, see *Eimeria stiedæ*
- Coccidium perforans*, see *Eimeria stiedæ*
- Coccidium tenellum*, see *Eimeria stiedæ*
- Cocks, old, killing, down, 389, 442, 481
 uselessness of, 472
- Collision with wire, 153
- Committee, list of names, ii. 1 ff
- Corn feeding, 25, 81-82, 113
 relation to disease, 178 ff
 injury from, 81, 82, 382
 unusual effect on blackgame, 161
 poaching and, 452
- Correspondents local, list of, ii. 1 ff
- Crop, 101, 102, 111
 never contains water, 102
 inflammation of, 111
 accidental injury to, 168-169
 shot pellets in, 169
- Crop contents, 67
 weight of, 67
 table of materials examined, 68
 analysis of specimens from chicks, ii. 86-90
 table of weights, 69
 tables of contents, 70, 76
 table of monthly averages, 79
 chart of percentages of foods, 80
 of Rype, 177
 of Blackgame, 424
 schedule of, of all specimens examined, ii. 27-85
- Crossing of blood, 479-482
- Crow, as vermin, 448
- DAVAINA CESTICILLUS*, 341
 morphology, 341

- Davainea cesticillus*—continued
 rare in Grouse, 342
 intermediate host, 342
- Davainea echinohothrida*, 339
 lesions produced by, 339
 similarity to tuberculosis, 340
 economic importance, 340
- Davainea tetragona*, see *D. echinohothrida*
- Davainea urogalli* (Large Tapeworm), 334 ff
 effect on host, 113-115, 277
 habitat, 105, 285, 334
 in caeca, 290
 post-mortem migration to caeca, 334
 and bacterial infection, 290-295
 and mortality, 295
 seasonal prevalence, 297 ff
 morphology, 336
 sexual organs, 337
 intermediate host not discovered, 338
- Dew, 94
- Dew-pans, 389
- Diarrhoea, "white," 259, 260, 268
- Digestion, process of, 105 ff
 chemical reactions in, 104-106
- Diptera*, parasitic, 358 ff
- "Disease," 135 ff, 444 (see also Strongylosis)
 history of, 185 ff, 444
 early records, 185-186
 in eighteenth century, 185-186
 former writers on, 147, 148, 185, 187 ff, 378
 distribution of (maps), 187; ii. 137 ff
 no district free from, ii. 138
 no periodicity of recurrence, 379
 "years," 395; ii. 138
 summary of problems, 149, 202
 of conclusions, 150; ii. 140
 relation to corn-feeding, 178 f
 William Colquhoun's pamphlet, 179-181
 John Colquhoun ("Moor and Loch"), 178
 "Klein's Disease," 123, 188 ff, 194-200, 274, 379
 not met with in Inquiry, 200, 204, 290, 379
 Cobbold's theory, 188 ff, 194, 274, 396
 other views, 188-197, 378-382
 Tom Speedy, 181, 193, 195
 Dr Andrew Wilson, 195-196
 Tegetmeier's theory, 490
 Committee's provisional view, 189-190, 199 ff
 "final view, 204, 373
 not due to tapeworms, 193
 not due to *Bacillus coli*, 200, 275, 297
 not due to "preservation," 185, 444
 not connected with geological formation, ii. 139
 due to Strongyle worms in caeca, 116, 204, 373
 pathology, 273 ff
 cultures from internal organs, 279 f
 methods of examination, 278 ff
 effects of on sexes, 50, 51, 377; ii. 121
 always causes wasting, 205, 277
 relation to weight, 130, 135, 138, 140, 194, 277, 299, 377, 380, 471
 undersized and late birds, 471
 dissection a test for, ii. 138
 no autumn outbreaks, 49, 51, 128; chart, 139, 455
 artificial remedies for, 382
- "Disease"—continued
 relation to wet moors, 413
 relation to rainfall, ii. 140
 rapid recovery from, 477
 sickly birds in autumn convalescent, 128, 469
- Diseases, minor, of Grouse, 150
 of skin, 183-184
- Distribution of Grouse, 1, 3
- Draining, 413
 advantages of, 389, 413 ff
 methods recommended, 413
 by gamekeepers, 440
 to discourage heather beetle, 423
- Driving, see Grouse-driving
- Droppings, hard, 107
 soft, 107, 180; ii. 92
 "clocker," 110, 134
- Drought, 16, 172
 favours Coccidiosis, 264
 unfavourable to *Trichostrongylus*, 233
- Dung-fly, 360 ff
 as carrier of coccidian spores, 246, 262
 not intermediate host of cestodes, 345
 in Grouse droppings, 360
 larvæ, 361
 morphology, 361-362
- Duodenum, 103, 104, 284-285
 habitat of small tapeworm, 104
 effect of parasites on, 113-114
- EAGLE, 19, 444, 449
- Ectoparasites, 348 ff
 relation to endoparasites, 365
- Eggs, number of, 8
 depends on healthiness of stock, ii. 128
 colour of, 8
 intervals in laying, 8
 size and colour, 9
 effect of weather on, 9; ii. 128
 of snow, 9, 10; ii. 129
 of frost, 10, 11, 12; ii. 129
 of wet, 9, 10; ii. 129
 hatching of, 13
- Egg stealing, 453
- Egg changing, 479
- Eimeria avium*, see *Coccidium avium*
- Eimeria cuniculi*, see *Eimeria stiedæ*
- Eimeria falciformis*, 240
- Eimeria schubergi*, 236, 240, 249
- Eimeria stiedæ*, 240, 242-243, 245, 254, 257
- Employees on Grouse-shootings, 495
- Endoparasites
 relation to ectoparasites, 365
 seasonal prevalence of, 298
- Eosinophilia* in Grouse, 231, 316
- Euston, or "Stetchworth" system, 439
- Extra-uterine gestation, 183
- FEEDING, hours of, 19, 20, 67, 109
 during incubation, 110
- Feet, accidental injury to, 167, 170
- Fences, danger from wire, 20
 "bushing" of, 20, 441, 502
- Fencing of burnt areas from sheep, 501

- Fighting, mortality from, 181
Filaria smithi, 218
 Fires, accidental, 400
Flagellata, 325
 Fleas on Grouse, 362 ff
 Flies on Grouse, 358 ff
 Flight, powers of, 26
 Flooding, 15, 16; ii. 129
 Food, heather nearly all-important, 70, 81, 398; ii. 129
 but not indispensable, 69, 70
 various, 70, 77, 84-87
 heather seed, 74, 76, 153; ii. 129
 berries, 73, 74, 455
 insects, 77, 78, 88, 89, 90, 100, 369
 corn, 25, 81, 82, 113, 382
 percentages in summer, table, 70
 winter, nature of, 25, 75
 greater quantity required in winter, 79, 132, 399
 percentages in winter, table, 76
 proportion of animal and vegetable, 90-91
 chemical constituents, 100
 monthly dietary, 83 ff
 Food areas, overcrowding on, 81, 136, 376, 379, 400
 Food plants, list and description of, 83-87
 Food supply
 heather burning and, 898, 400
 conditions affecting stock, 455
 relation of to migration, 81
 Foreign species, introduction of, 53
 Foster mothers, unsuccessful, 485-486
 Fox, methods of destruction, 445
 Fresh blood, introduction of, 28, 53, 475, 477-478
 unnecessary where birds migratory, 477
 birds apt to wander, 477
 risks of introducing, 478
 objections to introducing, 479
 Frost, effect of on eggs, 10, 11, 12, 173; ii. 129, 132 ff.
 on pheasants' eggs, 11; ii. 134
 Analysis of observations on, ii. 132 ff
 interrupting breeding, ii. 133
 result of observations, ii. 136

GAMASUS COLEOPTRATORUM (beetle-mite) on Grouse, 365
 Gamedealers' licences, 452, 499
 Gamekeepers, 430 ff
 importance of, 430
 should be owner's servants, 430, 432
 relations with agricultural tenants, 432
 terms of service, 433
 should not be paid in "kind," 433
 married and unmarried, 433
 pension fund, 433
 number required, 434
 Head, 434-435
 Under, 434-435
 area under one man's control, 434-435
 selection of, 435
 essential qualifications, 435
 personal qualifications, 436

 Gamekeepers—*continued*
 the "ideal" and the inefficient, 436-437
 training of young, 436
 importance of keenness in, 436
 duties, 438 ff
 in "off" season, 438
 in nesting season, 438 ff
 "Stetchworth" system, 438-439
 improving nesting ground, 440
 drains and springs, 440
 grit supply, 440
 vermin killing, 441
 butt building, 441
 "bushing" fences, 441
 bracken, destruction of, 441
 estimating stock, 441
 observing nests and broods, 459
 in shooting season, 442 ff
 Grouse driving, 436-437
 cocks, killing down, 442, 453
 Autumn heather-burning, 442
 in Winter, 442
 vermin tracking in snow, 443
 total of wages paid to, 495
 Game-laws Commission, 394
 Game licences, economic value of, 499
 "Gapes" in Grouse, 213
 Geological formations
 in Scotland, ii. 139
 no relation to "Disease," ii. 139 f
 Gizzard, 102, 103, 106, 111
 in Grouse chicks, schedule of all specimens examined, ii. 27-35
Goniodes tetraonis (bird louse) on Grouse, 348 ff
 habits, 349
 morphology, 349-356
 eggs, 356
 and skin disease, 183-184
 Grazing rents and sheep rents, 396
 Gregarines in Grouse, 330
 spores in alimentary canal, 330
 Grit, 94 ff
 in Grouse chicks, 18
 eagerly sought for, 20
 size of, 95
 weight of, 95
 quantity of, 95
 geological constituents of, 95
 quartz, always preferred, 96, 97, 99, 102
 garnets and glass beads rejected, ii. 94 f
 in partridge and pheasant, 96
 artificial introduction of, 97, 440
 during snowstorms, 177; ii. 94
 effect of grit-starvation, 97; ii. 92 ff
 control over loss of, 97, 98, 114; ii. 92 ff
 berries as substitute for, 98, 103
 in blackgame, 99
 functions of, 100
 shot pellets as, 103, 169
 Grouse, history of name, 1
 distribution, 1, 3
 confined to Britain, 53
 acclimatisation, 1, 2
 economic importance, 2, 492 ff

- Grouse—*continued*
 systematisation, 2, 3
 plumage, 3, 29 ff
 habits, 4
 food, 4, 67 ff
 feeding habits, 19, 20, 67, 109
 life history, 5 ff
 pairing, 5
 pugnacity, 6, 181
 nesting habits, 6, 7, 13
 eggs, 8, 9
 care of brood, 14
 dangers to chicks, 14
 habits of chicks, 14
 migration, 14, 15
 wildness, 18
 hardiness, 21; ii. 114
 longevity, 28
 minor diseases, 150
 parasites, 347
 resistance to disease, 376, 377
 recuperative powers, 151, 153
 effect of weather on, 9; ii. 128 f
 numbers vary with rainfall, ii. 140
 methods of shooting, 460 ff
 netting, 453
 economic value per brace, 492
 (See under separate headings)
- Grouse chicks, 14 ff
 habits, 14
 dangers to, 14
 disappearance of, 14-16, 264; ii. 120, 124, 130, 132
 drowning, 15; ii. 129 f
 food, 17, 18
 insect, 88, 89, 90
 vegetable, 90, 92
 table of, 90
 flight of, 19
 liable to Coccidiosis, 261
 "Grouse Disease" see "Disease"
- Grouse driving, 460 ff
 advantages of, 389, 462, 480
 disadvantages, 462
 effect on yield, 463
 history of, 463
 results in England, 464
 in Scotland, 464
 rules for, 464
 gamekeepers' duties, 437
 management of, 437
 heather-burning for, 404
 minor days, 465
 young and old killed by, table, 474 f
 crossing of blood by, 479-482
 on Broomhead Moor, 480
 wages paid for, 496
- Grouse fly (*Ornithomyia lagopodis*), 330, 358 ff
 morphology, 358
 habits, 359
 blood-sucking by, 330
 carrier of protozoal parasites, 331
- Grouse in captivity, 483 ff
 coops, 484
- Grouse in captivity—*continued*
 food, 484, 487
 of chicks, 488
 water, 484
 grit, 487
 mating experiments, 487
 change of ground, 488
 late nesting of, 488
 Coccidiosis in, 490
- Grouse moors, 393
 of small agricultural value, 491-492
 economic value of, 414 ff, 492
- Grouse shooting; in former years, 390
 to regulate stock, 456-458, 479
 no interference with agriculture, 491
 indirect value of, 479 ff
 cost of, 498
 methods of, 460 ff
 over dogs, 460
 advantages, 461
 disadvantages, 461
 rules for, 461
 young and old killed by (table), 474
 driving, see Grouse driving
- Grouse shootings, value of, 491 ff
 economically profitable, 491
 ground of small value, 491 f
 valuation of, 493
 rents of, 494
 employment on, 494-496
 benefits to district, 496-498
 summary of values, 498
- Gulls, as vermin, 450
- HÆMOPROTEUS MANSONI*, 323
 intermediate host, 323
- Hand-rearing, 479 ff
 coops, 484; ii. 91
 food, 484
 water, 484
 successful, 485
 result of experiments, 489, 490
 of grit starvation, ii. 92 ff
 infection with Strongylosis, ii. 100 ff
 " with Coccidiosis, ii. 103 ff
- Hatching, date of, 7
 period of incubation, 13
 early, value of, 470 ff; ii. 130
 late, result of, on stock, 140, 173
 on weight, 140
- Hawks, not all are vermin, 450
- Heart, 117
- Heath, cross-leaved (*Erica tetralix*), 77, 84
- Heather, bell (*Erica cinerea*), 84
- Heather, common (*Calluna vulgaris*)
 importance of as food, 70, 81
 not indispensable, 69
 old, as food, 77, 78, 399, 455
 objections to, 408
 uselessness of, 409
 various types, 71 ff
 winter, 71, 175
 dwarf, 71
 short and long, 71, 378

Heather, common—*continued*

- young, most nutritious, 72, 73, 465; ii. 129
- culture, 72
- growth from seed, 73, 400, 402
- „ from root, 73, 400
- seedlings eaten by sheep, 73, 402
- and by young Grouse, 73
- not by adults, 73
- blossom, 74
- seed, 74, 133; ii. 129
- ripening of, 74
- not eaten after January, 75
- “frosted,” 174, 378
- term defined, 175
- effect of frost on, ii. 130
- good growth, effect of on stock, ii. 129
- good grain year, good year for, 75; ii. 130
- effect on of weather, ii., 128
- burning, *see* Heather-burning
- raking, in time of snow, 176, 442
- Heather-beetle (*Lochmea suturalis*), 414 ff
- as causing “frosted” heather, 176, 414 ff, 423; ii. 124
- former observations of, 416 f, 426
- distribution, 414, 422
- correspondence regarding, 415 ff
- types of heather attacked by, 415, 423
- action on plant, 417
- quantity to acreage, 418
- records of damage by, 415-422
- date of injury, 422
- methods of search for, 417, 418
- analysis of heather samples, 418
- life history, 422, 426 ff
- incomplete, 429
- influence of climate on, 423
- „ of rainfall on, 423
- moisture favourable to, 423
- experiments with, 423, 426 ff, 429
- eaten by blackgame, 424
- methods of destroying, 423-425
- morphology, 426 ff
- characters, 427
- allied forms, 426
- hibernation, 429
- pairing, 429
- Heather-burning, 392 ff, 443
- history of, 393-396
- “keeper's delight,” 393-395
- beneficial to both Grouse and sheep, 395, 405 f
- sheep-farmers' views, 405 f
- co-operation by shepherds, 406
- in interests of landlord, 431
- „ of shooting-tenant, 431
- to destroy “disease,” 233, 397
- to discourage heather-beetle, 403, 425
- to foster healthy stock, 399, 431; ii. 131
- for future years, 443
- to provide food supply, 398
- in interests of sport, 404
- in strips, 401
- „ large patches, 401
- „ small patches, 396, 401

Heather-burning—*continued*

- rules, 396 f, 406
- labour required, 397
- expense of, 409
- areas, apportionment of, 399, 401
- rotation of, 399-401, 407
- estimating, 397 f, 408
- measurement of, 399
- example of scheme, 408 f
- choice of rotation, 408
- methods of burning, 397, 401 ff
- burning against the grain, 402
- back-firing, 402
- second burning, 402
- old and young heather, 400, 406
- treatment of steep faces, 402
- of flow ground, 403
- of north slopes, 403
- of knolls, 403
- of peat hags, 403
- of “grey” heather, 403
- of burns and streams, 404
- of “white grass,” 411
- of “green ground,” 411
- statutory seasons for, 404
- “Spring” and “Autumn,” 404
- not after nesting begun, 470
- Autumn burning, 404 ff, 442
- periods of re-growth after, 408
- objections to, answered, 409
- Hedgehog, as vermin, 447
- Helminthiasis, *see* Tapeworms, etc.
- relation to weight, 143
- blood-count in, 316
- Hens, old, uselessness of, 472
- Heterakis papillosa*, in Grouse, 217 f
- common worm in poultry and pheasants, 217
- synonymy, 217
- “Hogging”—effect on heather growth, 501
- House fly, (*Musca domestica*)
- as carrier of coccidian spores, 262
- Hymenolepis microps* (Small Tapeworm), 342 ff
- habitat duodenum, 104, 105, 342
- numbers present, 342
- effect on tissues, 113-115
- difficult to detect, 342
- not directly associated with mortality, 294
- nor with bacterial infection, 290-294
- seasonal prevalence, 277, 285, 297 f
- effect on host, 113-115, 277
- morphology, 343
- sexual organs, 343-344
- intermediate host not discovered, 344-346
- IMMIGRATION of fresh stock, 476-477
- evidence of, 477
- Incubation, effect of on weight, 140
- period of, 13
- Insects, as food, 77, 88-90, 100, 369; ii. 86-90
- parasitic, 348-360, 362 ff
- as carriers of coccidian spores, 262
- Intestine, small, 104, 106, 115, 285
- upper and lower portions, 105
- habitat of large tapeworm (*Davainea*), 105

- Intestine, small—*continued*
 inflammation of, 115
 convolutions in, 106
 Intussusception, 116, 122
 Isolated moors, 478
Ixodes ricinus (Dog-tick), on Grouse, 363-365
 as nymphs and larvæ, 363
 causing acute skin disease, 183-184
- JACKDAWS, as vermin, 449
 beneficial effect of reducing, 449
 "Juggling," 21
- KESTREL, beneficial, 450
 Kidneys, 126
 cultures from, 279
 "Klein's Disease," 123, 188 ff, 194-200, 274, 379
 not met with in Inquiry, 200, 204, 276, 299, 379
- LATE shoots, 458-459
 Leg-feathering, 31, 36, 40, 45, 49, 51
Leucocytozoon lovati, 318 ff
 life history, 319 ff
 staining, 319
 morphology, 320 ff
 gametogony, 320
 possible periodicity, 321
 schizogony, 322
 intermediate host, 322
 association with Coccidiosis, 319
 blood-count in, 315
 Lice on Grouse, 348 ff, 356 ff (see *Goniodes*, *Nirmus*)
 Liver, 104, 106 f, 117
post-mortem changes in, 117, 125, 277
 effect of Coccidiosis on, 125
 not affected by Strongylosis, 125
 cultures from, 280
Bacillus coli in, 282, 289, table, 290
Lochmæa suturalis, see Heather-beetle
 Longevity of Grouse, 28
 Lungs, 123 f
post-mortem appearance, 123, 125
 living parasites in, 124
 cultures from, 279
- MALLOPHAGA (Bird-lice), on Grouse, 348 ff
 Maps, showing incidence of disease, ii. 137 ff
 deductions from, ii. 140
 Mating, experiments in, 487
 Mesentery, 104
 Migration, 25 ff
 seasonal, 6, 25 f, 382
 wholesale, 25 f, 389, 466
 relation to food supply, 81
 induced by heather-beetle, 414
 affecting stock-regulation, 466 ff
 not universal, 476-478
 as effecting crossing of blood, 476, 481
 as re-stocking vacant ground, 477
 Mites (*Aleurobius farinæ*) on Grouse, 364-365
Monocercomonas eberthi, see *Trichomonas eberthi*
Monocystis sp., 330
 spores in alimentary canal of Grouse, 330
- Moor management, 372 ff
 defined, 377
 examples of, 383 ff
 deductions from, 389
- Mortality
 in April and May, 133, 140
 in June and July, 36
 seasonal, in cock and hen, 136, 140, 377
 causes of, 147 ff
 accidental, 153
 in blackgame, 158
 from fighting, 181
- Moult, 29 ff
 normal, 135, 137
 deferred, 31, 37, 52, 182
 of cock and hen different, 34, 43, 128, 137
 of ptarmigan, 41
 explanation of terms, 43
 effect of disease on, 49, 127
 effect of, on weight, 135, 137, 141
 risks attending, 177, 182
- Musca domestica* (House-fly)
 as carrier of coccidian spores, 262
- NEMATODES, non-parasitic, 375
 larvæ on heather everywhere, ii. 100
- Nesting, 7 ff
 sites, 7; ii. 136
 date of, 7
 early, advantageous, 470; ii. 130
 second, 471
 strain of, 471
 "Nesting-patch" on hen, 47, 48, 52
- Netting Grouse, 453
Nirmus cameratus (Biting louse), on Grouse, 356-358
 synonymy, 357
 habits, 357
 morphology, 357
 eggs, 357
- OBSERVATION area, 483 ff
 Oesophagus, 101, 111, 112
 congestion of, 112
 Old and young birds, 473
 proportions in "dogging" and "driving," 474
 Old birds undesirable, 472 f
Ornithomyia lagopodis, see Grouse-fly
 Ovaries, 60 f, 127
 effect of "disease" on, 127
- Over-crowding on food areas, 81, 136
 Over-sitting, 473
 Over-stocking, relation to disease, 382 ff
 Oviduct, 61
 effect of "disease" on, 127
- Oxyuris ambigua* (nematode worm), 297
 no relation to bacteria in tissues, 297
- PACKING, 23 f, 25
 reasons for, 400
 in relation to age and sex, 475
- Pairing, 5
 effect of weather on, 5
 effect of snow on, 5
 sometimes postponed, 5

- Pancreas, 104, 114
 cultures from, 280
 Partridges,
 methods of stock management, 439, 459
 Peregrine, falcon, 448
 Physiology, 100 ff
 of pigment production, 39 f
 Pigmentation, physiology of, 39 f
 of feathers, 37 f, 46
 in relation to "wear and tear," 47
 of eggs, 38
 "Piners," how produced, 471
 in autumn, 50, 129, 133, 182
 description of, 139
 in spring, 173
 Plumage, 29 ff
 local variations of, 3, 4, 42, 53 ff
 in cocks, classification of types, 55 f
 red type, 56
 black type, 57
 white spotted type, 57
 in hens, classification of types, 58
 red type, 58
 black type, 58 f
 white-spotted type, 59
 buff-spotted type, 59
 buff-barred type, 59 f
 abnormal variations, 60
 uniformity the general rule, 44
 seasonal changes, 29 ff
 in cock, 29, 34-42
 "Winter" and "Summer," 29
 effect of disease on, 30 f, 33, 127 f
 Ogilvie-Grant's theory, 31, 34, 37
 Millais's theory, 31, 37, 40
 "eclipse," 32 ff, 37, 48
 appellation inexact, 33
 "Spring" and "Autumn," 32
 in allied species, 34, 41
 in hen, 38 f, 43-53
 re-pigmentation, 37, 40, 128
 Metchnikoff's theory, 37
 as guide to sex, 62
 as guide to age, 48, 63
 Pneumo-enteritis, 490
 Pneumonia, 123 f, 125
 never observed, 200, 204, 276, 299
 Poached game, facilities for sale of, 452
 Poachers, 450 ff
 professional, 450, 452
 occasional, 450, 452
 prevention of, 451
 in former days, 451
 snaring on stooks, 451
 "becking," 452
 netting, 453
 egg-stealing, 453
 Poisoning, 169 f
 septic, in Grouse, 170
 Polecat, 447
 "Preservation-theory" of "Grouse Disease," 185, 444
 Primary feathers, growth of, 64 f
 diagram, 64
 Protozoa, 318 ff
 bibliography, 332
 Proventriculus, 101, 106, 111
 Psorospermium avium, see *Coccidium avium*
 Psorospermiosis see Coccidiosis
 Ptarmigan, moults of, 41
 RAINFALL, effect on heather-beetle, 422
 relation to yield of Grouse, ii. 140
 Raven, as vermin, 449
 Rectum, 104, 106, 110
 inflammation of, 116
 Re-pigmentation of plumage, 37 ff, 46, 128
 Metchnikoff's theory, 37
 Millais's theory, 40
 Rhizopoda, 323 (see *Amœba lagopodis*)
 Rook, as vermin, 449
 Rotation, in heather-burning, 407
 SCATOPHAGA STERCOBARIA, see Dung-fly
 Scent, loss of while sitting, 13
 Sex, methods of ascertaining, 60 ff
 in relation to plumage, 61 f
 " to weight, 134, 140
 " to packing, 475
 Sheep, destructive to seedling heather, 73, 402
 advantageous on heather ground, 500
 may kill out heather, 500
 fencing burnt areas from, 501
 Sheep-drains, 15, 169
 Sheep-rents and Grazing-rents, 394
 Sheep-stocks, notes on management, 499
 control of, 501
 Shooting lodges, 493
 Shot, wounds from, 151, 153, 162 ff
 alleged poisoning by, 169 f
 Skin disease, 183 f
 Snaring on corn stooks, 452
 Snow, effect on pairing, 5
 on nesting, 10 ; ii. 129
 on healthiness of stock, 22, 381 ; ii. 130
 on migration, 6, 381
 on heather, 176, 381
 "jugging" in, 22
 breaking of surface, 176, 442
 vermin tracking in, 443
 "Soft-shell," 183
 Specimens examined, schedule of, ii. 27-85
 Spirochæta eberthi, see *Trichomonas eberthi*
 Spirochæta lagopodis, 323 ff
 staining, 324
 characters, 324
 schizogony, 324
 effect on host, 325
 intermediate host, 325
 blood count, when present, 314
 Spirochæta lovati, 327 f
 staining, 327
 in caecal contents, 327
 structure, 327
 schizogony, 328
 Spirochetacea, 323-327
 Sporozoa (blood parasites) of Grouse, 318-325
 Spleen, 126

Spleen—*continued*

- as affected by *Strongylosis*, 126
- cultures from, 280

Staff, list of, ii. 1

"Stetchworth" or "Euston" system, 439

Strongylosis, 207 ff

- the "Grouse Disease" of adults, 116, 373
- in normal birds, 118, 300
- almost universal in Grouse, 196, 209, 286, 374, 376

Cobbold's discovery of, 188 ff

a progressive ailment, 118, 376

due to vast numbers of *Strongyli*, 286, 376

occurs in caeca, 109, 111, 117, 219, 316, 377

pathology, 119 f, 230 ff, 273 ff, 374

effect on caeca, 113, 123

post-mortem appearance, 286 ff

inflammation and fibrosis, 289

effect on moult, 36, 50 f, 127

on spleen, 126

on reproductive organs, 127

no effect on liver, 125

affecting weight, 141, 194, 204

examples of, 121 f

seasonal mortality from, 135, 141

recovery from, 120

toxæmia in, 109, 118, 301

helminthic toxins in, 208

relation to *Bacillus coli* in tissues, 290 ff

eosinophilia in, 231, 316

blood-count in, 316

infection, artificial, 229 ff; ii. 100 ff

„ natural, 136, 232 f

remedial measures, 231

relation to food supply, 232, 234; ii. 130

Strongylus pergracilis, see *Trichostrongylus pergracilis*.

Stoat, methods of destruction, 446

Stock management, 454 ff

meaning of term, 454

statistics, 455

generalisations, 456

examples of typical moors (table), 456 f

the "ideal," stock, 454, 467

in relation to acreage, 455

"Winter" and "Summer," 81, 455, 465

dependent on winter food supply, 455, 458, 465; ii. 131

ascertainment of, 458-459

regulation by shooting, 456 ff, 479

proportionate yield, 455

on let moors, 458

in good season, 460, 467

in bad season, 461, 467

methods, 460 ff

healthiness to be considered, 469; ii. 129

and results of nesting, 459

migration as affecting, 466-468

policies sometimes adopted, 466 f

necessity for co-operation, 468

rules for, 468 f

objects to be aimed at, 468

large "Winter," undesirable, 466

methods of reducing, 466

maintenance of heather, 469

Stock management—*continued*

sickly birds in autumn may be spared, 469

"cheepers" should be killed out, 469 ff

old birds undesirable, 472 ff

proper ratio of young and old, 473, 474

artificial improvement, 475

by fresh blood, 476 ff, 481

migration and re-stocking, 477

where Grouse non-migratory, 478

egg-shifting, 479

importing birds and eggs, 479

hand-reared birds, 479

summary of conclusions, 479

Subscribers, list of, ii. 10

Syngamus trachealis ("Gapes-worm"), in Grouse, 213

TAENIA CALVA, see *Davainea urogalli*

Tænia cesticillus, see *Davainea cesticillus*

Tænia microps, see *Hymenolepis microps*

Tapeworm, see *Cestoda*

Tapeworm, large, see *Davainea urogalli*

small, see *Hymenolepis microps*

Temperature (body), of Grouse, ii. 110

Tentsmuir, 93; ii. 139

Testes, 60 f, 126 f

effect of disease on, 127

Threadworm, see *Trichostrongylus* and *Trichosoma*

Ticks, on Grouse, 363 (see *Ixodes*)

Toxæmia, 109, 118, 204, 301

Toxins, helminthic, 208

Trichomonas eberthi, 325

synonymy, 325

in caecal contents, 325

staining, 326

structure, 326

schizogony, 326

encystment, 326

Trichosoma longicolle, 214 ff

synonymy, 214

less common than *Trichostrongylus*, 114

habitat duodenum, 104, 113, 217

structure, 215

morphology, 215, 217

pathological effect small, 217

but allied to dangerous parasite in man, 217

Trichostrongylus pergracilis, 218 ff, 375

cause of "Grouse Disease" in adults, 116, 373

habitat caeca, 109, 111, 116 f, 219, 377

numbers present, 286, 316

methods of counting, 283

almost always present, 196, 209, 286, 374, 376

allied species, 207, 208, 212 f

synonymy, 207 ff

characters, 207 f

life history, 218 ff, 228 f

development, 218 ff

within host (*morula*), 219, 375

outside host, 319 f

artificial cultivation, 220

ovum, development of, 221

moisture necessary to, 226, 233, 375

effect of drought on, 233

embryo, structure of, 222

first ecdysis, 224, 375

Trichostrongylus pergacilis—continued

- quiescence during cold weather, 233
- metamorphosis, 224, 375 ; ii. 101
- larvæ, 225
 - encystment, 225, 375
 - migrations, 224, 375
 - on heather, 225-228
 - experimental administration of, 229 f, 374 ; ii. 100 ff
 - effect of frost on, 232, 375
 - „ of drought on, 232, 375
 - „ of sea spray on, 375 ; ii. 139
 - maturity and reproduction, 229, 376
 - methods of destruction, 234

Trypanosoma eberthi, see *Trichomonas eberthi*

UNDERSIZED birds, 377, 472

VERMIN, 16, 177, 443 ff

- keepers' duties, 443 ff
- “balance of Nature,” 443
- sometimes beneficial, 445
- vermin-killing and “disease,” 444
- tracking in snow, 443
- methods of destruction, 444 ff
- golden eagle, 19, 444, 449
- fox, 445 f
- stoat, 446
- weasel, 447
- hedgehog, 447 f
- cat, wild, 447
- peregrine falcon, 448
- crow, 448
- rook, 449
- jackdaw, 449
- raven, 449
- hawks, 450
- gulls, 450

WATER-DRINKING by Grouse, discussed, 18, 93 f

Water drinking—continued

- by adults, 18
- by chicks, 18, 472
- in hand-reared birds, 481
- in sickness, 102
- Grouse do not often die of thirst, 264
- artificial supply, 93 f, 389
- Weasel, as vermin, 447
- Weather, 9 ff

- effect of, on eggs and young, 9 ; ii. 130
 - on nesting, 10 ; ii. 130 f
 - on breeding, 12, 172
 - on chicks, 13 f ; ii. 130
 - on health of stock, ii. 128, 130
 - on heather, ii. 130

Analysis of, during years of Inquiry, ii. 113 ff

Weight of Grouse, 130 ff

- as test of disease, 130, 138, 140, 376, 380 ; ii. 111
- as sign of health, 377, 442, 471
- seasonal changes in, 130 ; chart, 131
- effect of courtship on, 134, 140
 - of moult on, 135, 137, 141
 - of late hatching on, 140
 - of incubation on, 140
- relation to disease, 135, 141 f, 277, 299
- effect of Coccidiosis on, 140, 204, 255 ; ii. 111
- of Strongylosis on, 141, 204 ; ii. 111
- of Helminthiasis on, 142
- conditions affecting, 140 f
- in relation to sex, 134, 140, 471
- local variations in, 143 ; table, 144 f
- records, 146
- “White diarrhoea,” 259, 260, 268
- Willow Grouse, plumage changes in, 41
 - crop contents, 177
- Wing feathers as guide to age, 64
- Wire, collision with, 153
- Woods as shelter, 22

Young and old birds, proportions of, table, 473

END OF VOL. I.

14 DAY USE
RETURN TO DESK FROM WHICH BORROWED

Biology Library

This book is due on the last date stamped below, or
on the date to which renewed.

Renewed books are subject to immediate recall.

APR 13 1965

Mr 30 '65 SH

DEC 15 1965

10 No '65 JN

LD 21-100m-6,'56
(B9311s10)476

General Library
University of California
Berkeley

